

NEOICHTHOLOGY OF BATS: MORPHOLOGICAL, ECOLOGICAL, AND PHYLOGENETIC
INFLUENCES ON TERRESTRIAL BEHAVIOR AND TRACKMAKING ABILITY WITHIN
THE CHIROPTERA

BY

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Submitted to the graduate degree program in Geology and the Graduate Faculty of the University
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ABSTRACT

Among living mammals, bats (Chiroptera) are second only to rodents in total number of species with over 1100 currently known. Extant bat species occupy many trophic niches and feeding habits, including frugivores (fruit eaters), insectivores (insect eaters), nectarivores (nectar and pollen-eaters), carnivores (predators of small terrestrial vertebrates), piscivores (fish eaters), sanguinivores (blood eaters), and omnivores (eat animals and plant material). Modern bats also demonstrate a wide range of terrestrial abilities while feeding, including: (1) those that primarily feed at or near ground level, such as the common vampire bat (*Desmodus rotundus*) and the New Zealand short-tailed bat (*Mystacina tuberculata*); (2) those rarely observed to feed from or otherwise spend time on the ground; and (3) many intermediate forms that demonstrate terrestrial competency without an obvious ecological basis. The variation in chiropteran terrestrial ability has been hypothesized to be constrained by the morphology of the pelvis and hindlimbs into what are termed types 1, 2, and 3 bats. This thesis examines the terrestrial ability of a number of species of Latin American bats belonging to the families Emballonuridae and Phyllostomidae that represent many of the ecological niches and all three pelvic and hindlimb morphotypes.

Within the species studied, terrestrial ability seems to be partially constrained by pelvic and hindlimb morphotype. The Type 3 bat *Desmodus rotundus* performed such typical quadrupedal gaits as the bound and the diagonal sequence walk. Among Type 1 bats, only *Carollia perspicillata* performed the diagonal sequence walk, and most Type 1 bats were restricted to an uncoordinated, asymmetrical gait herein termed the breaststrokelike crawl. Type 1 bats also frequently performed a nonambulatory behavior, termed the searching behavior,

which produced distinctive tracks. Type 2 bats in this study performed terrestrial behaviors more similar to those of Type 1 bats than to Type 3. The searching behavior produces distinct radial pes track patterns, and complete trackways are indicative of well-coordinated gaits like the bound. Trackways produced by all bats shared (1) elongate manus tracks, which may include the impressions of either digit I, the wrist and distal forearm, or both, and (2) pes tracks consisting of three or five parallel digit marks. These tracks and trackways can be used to establish criteria for identification of bat trace fossils in the geologic record, and eventually used for comparisons to pterosaur trace fossils to better understand their locomotor behaviors. As the only extant quadruped capable of powered flight, bats are likely the closest living analog for understanding pterosaur locomotion.

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CHAPTER 1. INTRODUCTION

This thesis arose out of an idea to study the neoichnology of bats (Mammalia: Chiroptera) as a proxy for pterosaur locomotion and behavior as reflected in such ichnotaxa as *Pteraichnus*, *Purbekopus*, and *Haenamichnus*. Little previous work had been conducted on the trackmaking ability of bats and eventually this aspect of the project proved to be substantial enough to warrant an entire thesis project; thus, the idea of using bats as a neoichnological proxy for pterosaurs was deemphasized. Future research will incorporate this thesis project with studies of pterosaur ichnofossils to attempt to better understand pterosaur locomotion and terrestrial behaviors, as bats—the only extant quadruped capable of powered flight—are the closest living analog for understanding pterosaur locomotion.

Previous studies of the terrestrial behavior of bats focused primarily on bats that are either known or presumed to be terrestrially competent (e.g., Altenbach, 1979; Riskin and Hermanson, 2005; Riskin et al., 2005, 2006; Schutt and Simmons, 2006). Far fewer studies have been conducted with bats presumed to be poor walkers (but see Dietz, 1973 and Riskin et al., 2005). This thesis is the first study to use a neoichnological approach to examine the tracks and trackways produced by bats maneuvering on the ground, although Lawrence (1969) and Dietz (1973) used various methods to attempt to understand the morphology of bat tracks and/or trackways. No bat tracks are known from the fossil record. Likewise, no studies have been conducted attempting to address any similarities between the terrestrial behavior and track morphology of bats and pterosaurs. As the only living quadrupeds capable of powered flight, bats are the most appropriate analog for understanding the terrestrial locomotion of pterosaurs as

preserved by their ichnofossils. The purpose of this thesis is to: 1) understand the track and trackway morphologies produced by bats maneuvering on the ground; 2) determine the variability present in terrestrial behavior and track morphology between terrestrially adept bats and those that are hypothesized to be poor and intermediate walkers; 3) determine the variability present in terrestrial behavior and track morphology between bats occupying different ecological niches; and 4) compare, if possible, the track morphology between bats and pterosaurs.

This research involves nine species of bats belonging to two families and five subfamilies of the diverse family Phyllostomidae: *Carollia perspicillata* and *C. sowelli* (Phyllostomidae: Carolliinae), *Desmodus rotundus* (Phyllostomidae: Desmodontinae), *Hylonycteris underwoodi* (Phyllostomidae: Glossophaginae), *Lonchorhina aurita* and *Micronycteris microtis* (Phyllostomidae: Phyllostominae), *Artibeus lituratus* and *Dermanura phaeotis* (Phyllostomidae: Stenodermatinae), and *Saccopteryx bilineata* (Emballonuridae). Four individuals of *C. perspicillata* were studied at the Lincoln Children's Zoo in Lincoln, Nebraska, USA, and all other bats studied were wild caught in mist nets at Reserva Ecológica Bijagual de Sarapiquí in northeast Costa Rica during late June and early July 2014.

Vaughan (1970) established criteria based on pelvic and hindlimb morphology that separated bats into three groups; he hypothesized these morphotypes had some bearing on their terrestrial abilities. Schutt and Simmons (2006) later termed these groups Types 1, 2, and 3. Under this scheme, Type 1 bats have the most gracile pelves and most caudally oriented hindlimbs, whereas robust pelves and laterally oriented hindlimbs characterize Type 3 bats. Type 2 bats are intermediate to the other two morphotypes. Presumably, such traits as robust pelves, complete fibulae, and laterally oriented acetabula allow for more effective terrestrial locomotion, however, this has not been thoroughly studied, especially among Types 1 and 2 bats. Of bats

used in this study, only *Desmodus rotundus* falls into the Type 3 category and only *Saccopteryx bilineata* falls into the Type 2 category; all other bats belong to the Type 1 group.

Bats are second only to rodents in total number of species among all living mammals. Modern bats occupy many trophic niches, including frugivory, insectivory, nectarivory, piscivory, carnivory, omnivory, and sanguinivory, and are present on every continent except Antarctica, as well as most remote islands (Rodríguez-Durán and Kunz, 2001; Bonaccorso and McGuire, 2013). Fossil bats show up nearly simultaneously in the early Eocene on all continents except Antarctica, and are already capable of flight and echolocation (with the possible exception of *Onychonycteris finneyi*; Simmons et al., 2008). The earliest bat body fossils are from Australia and Europe, with other early Eocene specimens known from Africa, North America, South America, and India (Hand et al., 1994; Tejedor et al., 2005; Smith et al., 2007; Tabuce et al., 2009; Ravel et al., 2011; Smith et al., 2012). Some early Eocene bat genera are present on multiple continents (e.g., Jepsen, 1966; Russell et al., 1973; Smith et al., 2007), and those specimens known from postcranial material appear, for the most part, anatomically modern. The origin and paleobiogeography of bats is, therefore, ambiguous.

No bat trace fossils are currently recognized in the rock record, although trace fossils attributed to all other groups of flying animals are known (e.g., Hasiotis, 2002; Kim et al., 2006; Lockley et al., 2008). Despite a lack of recognition, bat trace fossils are likely preserved in the fossil record due to their cosmopolitan distribution since the early Eocene and the wide variety of ecological niches occupied and terrestrial abilities displayed by living bats.

Chiroptera has long been considered on morphological grounds to be most closely related to the orders Primates, Scandentia (i.e., tree shrews), and Dermoptera (i.e., flying lemurs) in the superorder Archonta (McKenna, 1975; Szalay, 1977; Szalay and Drawhorn, 1980; Novacek and

Wyss, 1986; Shoshani and McKenna, 1998). Recent molecular studies, however, remove bats from Archonta and instead place them in the mammalian superorder Laurasiatheria (Fig. 1), along with pangolins (Pholidota), hedgehogs and shrews (Eulipotyphla), carnivorans (Carnivora), odd-toed hoofed animals (Perissodactyla), and even-toed hoofed animals and whales (Cetartiodactyla) (e.g., Lin and Penny, 2001; Murphy et al., 2001; Reyes et al., 2004; Zhou et al., 2011; Nery et al., 2012). The placement of Chiroptera within Laurasiatheria has been highly debated, with various studies placing bats as either sister to Eulipotyphla in the clade Insectiphillia (Madsen et al., 2001; Waddell et al., 2001), sister to Perissodactyla (Murphy et al., 2007), sister to a clade containing both Perissodactyla and Carnivora (Nishihara et al., 2006), sister to the Fereuungulata, which includes Carnivora, Cetartiodactyla, Perissodactyla, and Pholidota (e.g., Reyes et al., 2004; Arnason et al., 2008, Zhou et al., 2011), or sister to Cetartiodactyla (Hallström and Janke, 2008, Nery et al., 2012).

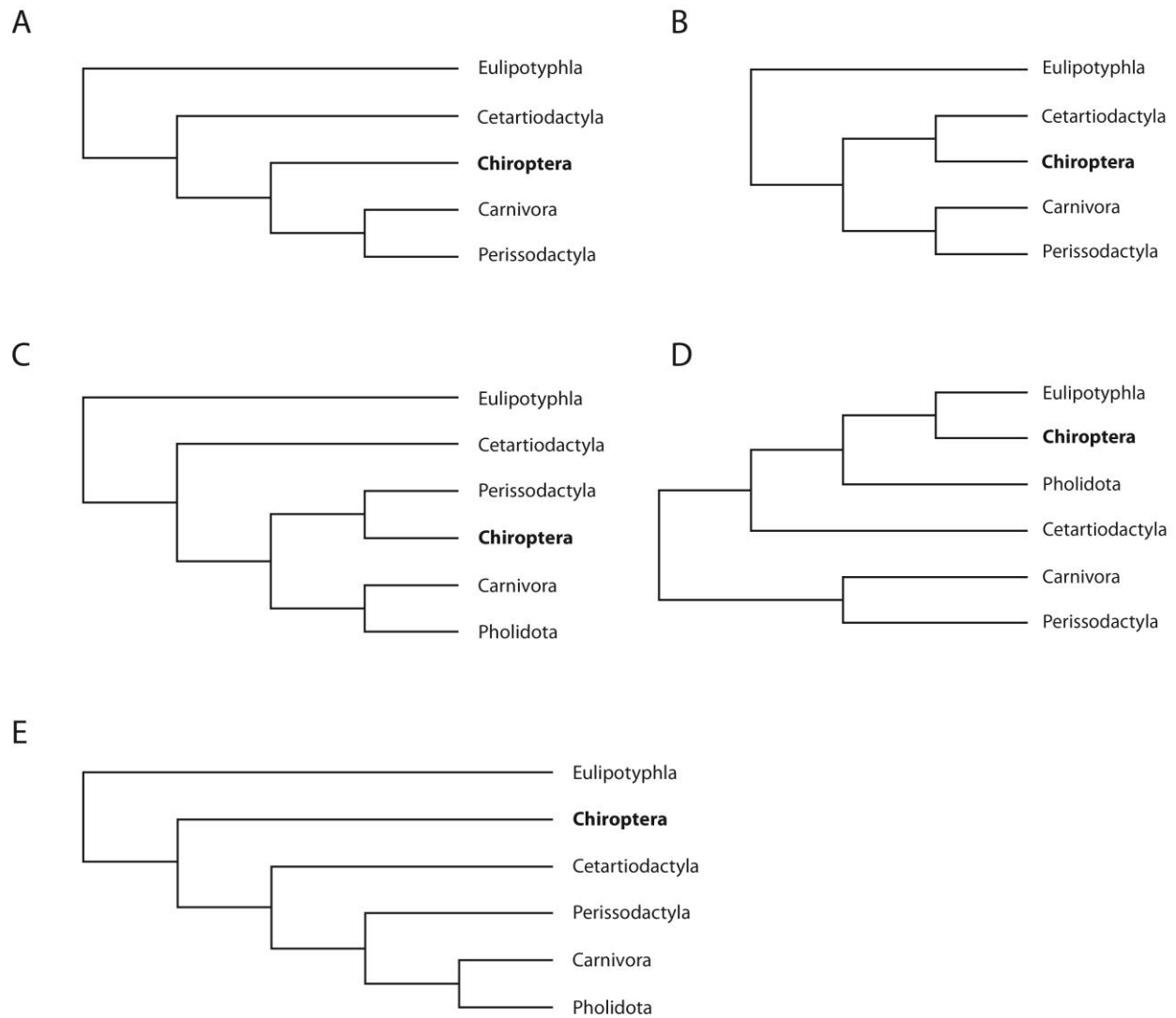


Figure 1. Examples of proposed phylogenetic placement of Chiroptera within the Laurasiatheria.

A) A member of Pegasoferae (Chiroptera + Carnivora + Perissodactyla), from Nishihara et al. (2006); B) Sister to Cetartiodactyla, from Nery et al. (2012); C) Sister to Perissodactyla, from Murphy et al. (2007); D) Sister to Eulipotyphla, from Madsen et al. (2001); E) Sister to Fereuungulata, from Arnason et al. (2008).

Within Chiroptera the traditional major division has been between the nonecholocating and strictly Old World family Pteropodidae, the sole member of the suborder Megachiroptera,

and the echolocating and cosmopolitan suborder Microchiroptera, consisting of all other bat families. Some studies have gone as far as to argue that Chiroptera itself is polyphyletic, with Megachiroptera more closely related to Primates than to Microchiroptera (e.g., Jones and Genoways, 1970; Pettigrew et al., 1989). Molecular phylogenetics invalidate both the traditional division and the Megachiroptera-as-flying-primates hypothesis, rendering the Microchiroptera paraphyletic by aligning the families Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, and Rhinopomatidae (superfamily Rhinolophoidea) more closely with the pteropodids than with the other microchiropterans (Van Den Bussche and Hofer, 2004; Teeling et al., 2005; Tsagkogeorga et al., 2013). The resulting suborders have been named Yinpterochiroptera, which includes the pteropodids and the five closely related former microchiropteran families, and Yangochiroptera, consisting of the remaining former microchiropteran families (Fig. 2; Springer et al., 2001; Teeling et al., 2002).

Yangochiroptera itself can be divided into three superfamilies: Emballonuroidea, Noctilionoidea, and Vespertilionoidea. Emballonuroidea consists of the sheath-tailed or sac-winged bats of the family Emballonuridae, which are cosmopolitan in distribution, and the slit-faced bats of the family Nycteridae, native to southeast Asia and Africa. Noctilionoidea includes the moustached bats of the family Mormoopidae, the bulldog or fishing bats of the family Noctilionidae, and the leaf-nosed bats of the family Phyllostomidae, all of which are native to the western hemisphere, as well as the short-tailed bats of the family Mystacinidae that are presently restricted to New Zealand, but at one point were also native to Australia (Hand et al., 2009). Vespertilionoidea includes the species-rich, cosmopolitan families Molossidae (free-tailed bats) and Vespertilionidae (evening bats), in addition to the bent-winged bats belonging to the family

Miniopteridae, native to the eastern hemisphere, and the funnel-eared bats of the family Natalidae, native to only the western hemisphere.

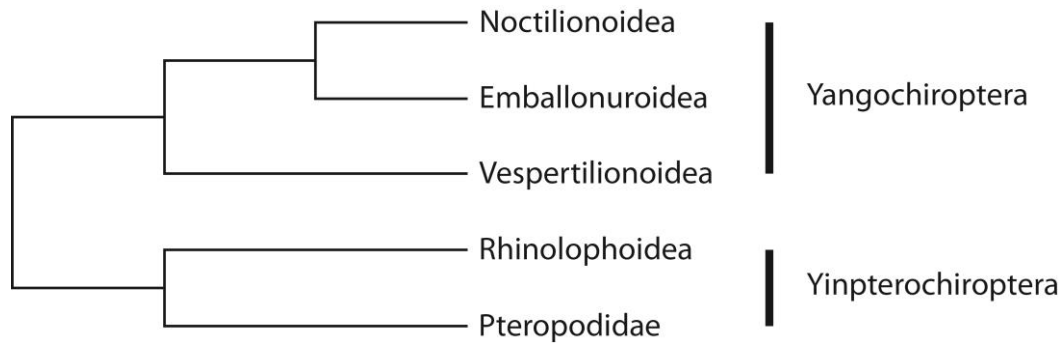


Figure 2. Hypothesized relationships of major groups within Chiroptera based on Teeling et al. (2002). The superfamilies Noctilionoidea, Emballonuroidea, and Vespertilionoidea constitute the suborder Yangochiroptera, and the superfamily Rhinolophoidea and family Pteropodidae constitute the Yinpterochiroptera.

The most thorough studies of terrestrial locomotion in bats focus primarily on two species, the common vampire bat (*Desmodus rotundus*; Phyllostomidae: Desmodontinae) and the New Zealand short-tailed bat (*Mystacina tuberculata*; Mystacinidae). Terrestrial locomotion in these taxa is relatively well understood and their capabilities for a range of terrestrial behaviors has been documented in experimental and wild settings for both species (e.g., Daniel, 1976, 1979; Altenbach, 1979; Greenhall, 1988; Riskin and Hermanson, 2005; Riskin et al., 2005, 2006). Both *D. rotundus* and *M. tuberculata* perform recognizable terrestrial gaits and spend considerable amounts of time on the ground while foraging for food.

Dietz (1973) conducted, perhaps, the broadest survey of terrestrial behavior among bats, sampling three phyllostomids (*Leptonycteris*, *Macrotus*, and *Artibeus*), two molossids (*Tadarida* and *Molossus*), and five vespertilionids (*Myotis velifer*, *M. yumanensis*, *Eptesicus*, *Pipistrellus* [now recognized as *Parastrellus*], and *Antrozous*); he, however, neither illustrated the behaviors recorded, nor included photographs in his manuscript. Dietz (1973) did observe the bats throughout their development and reported that juveniles tend to demonstrate more terrestrial competency than adults in such poor walking taxa as *Leptonycteris* and *Macrotus*. Among taxa surveyed, he observed *Antrozous* to be the best walker, with both molossids also capable of efficient terrestrial locomotion. The terrestrial ability of *Antrozous* supports observations of the bat foraging for insect prey from the ground (Orr, 1954). Other vespertilionids studied by Dietz (1973) exhibited variable, but more poorly coordinated gaits compared to *Antrozous*.

Lawrence (1969) studied the terrestrial locomotion of three species of vespertilionids native to Europe: the serotine (*Eptesicus serotinus*), the common pipistrelle (*Pipistrellus pipistrellus*), and the noctule (*Nyctalus noctula*). These bats performed several different gaits during the course of the study, including what was termed a walk (performed by *E. serotinus* and *P. pipistrellus*), a run (performed by *N. noctula* and *P. pipistrellus*), and an asymmetrical leap-frogging behavior (performed only once, by *N. noctula*). Lawrence (1969) also recorded bat tracks by covering the soil they walked across with talc powder, thus, providing the best approximation of bat track and trackway morphology to this point in time. His illustrations of these trackways and behaviors, however, were stylized rather than as photographs, videos, or outlines of the tracks produced.

Both Schutt et al. (1999) and Riskin et al. (2005) observed the terrestrial locomotion of the white-winged vampire bat, *Diaemus youngi*, and found it similar to *Desmodus rotundus*.

Diaemus youngi holds its body closer to the ground when walking, but performs similar behaviors to *Desmodus*, including hopping and a lateral sequence gait. Riskin et al. (2005) also observed the terrestrial behavior of two other species, the mormoopid *Pteronotus parnellii*, and the natalid *Natalus tumidirostris*. *Pteronotus parnellii* was reported to perform a variable gait in which the limbs were sprawled, the body was usually in contact with the ground, and the forearms were used to generate forward motion. *Natalus tumidirostris* did not attempt to crawl at all during the trials and the authors concluded that the species does not crawl.

Few researchers mention bat locomotion in passing, as part of larger studies. For example, Vaughan (1959) included observations of terrestrial locomotion in studies of three species of bats native to California: the molossid *Eumops perotis*, the phyllostomid *Macrotus californicus*, and the vespertilionid *Myotis velifer*. He reported that both *E. perotis* and *M. velifer* were capable of similarly coordinated gaits, although *M. velifer* held its body at an angle to the ground surface, whereas *E. perotis* held its body parallel and close to the surface. *Eumops perotis* was also capable of much more rapid locomotion and would walk for relatively long distances in order to reach its roost.

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CHAPTER 2. A PRELIMINARY ANALYSIS OF THE TRACKWAY-MAKING ABILITY OF BATS (PHYLLOSTOMIDAE, CAROLLIINAE)

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ABSTRACT

Extant bats (Mammalia: Chiroptera) exhibit a range of terrestrial abilities, with certain taxa known to be capable of coordinated walking or running gaits. Although many previous studies have focused on the terrestrial ability of bats known to be terrestrially competent, very little work has been conducted on the terrestrial ability of the vast majority of bat species and no previous studies attempted to describe and illustrate the tracks and trackways produced from a neoichnological perspective. In this study, four short-tailed fruit bats, *Carollia perspicillata* (Chiroptera: Phyllostomidae: Carolliinae), were subjected to walking trials on medium-grained sand with moisture levels of 12–21%. The bats exhibited three distinct locomotor behaviors: a diagonal sequence walk, a breaststrokelike crawl, and a hop interspersed within the other locomotor behaviors. These behaviors produced tracks corresponding primarily to the first digit of the manus, including lineations up to 10 times as long as they are wide and oriented parallel to the direction of locomotion, and arcuate furrows also corresponding to the first digit of the manus. Bats also produced pedal tracks, most often in association with a searching behavior in which the bats rapidly extended and retracted one hind limb in succession, producing several

subparallel pedal scratch marks. These marks consist of four to five parallel individual lineations that correspond to the pedal digits dragged through the sediment. This is the first study of the neoichnology of any bat species, as well as the first detailed description of the terrestrial ability of a hypothesized poor-walking species. Traces described in this paper can be used to help identify bat tracks and trackways preserved in the rock record in water-margin deposits of river, lake, and coastal plain settings, and may help to fill in gaps in the bat fossil record, which dates to the early Eocene.

INTRODUCTION

Extant bats are classified into three categories based on their pelvic and hindlimb (i.e., femur, tibia, fibula) morphology and presumed influence on their terrestrial competency (Vaughan, 1970). These groups are now known as Types 1, 2, and 3 bats (Schutt and Simmons, 2006). Type 1 bats are characterized by a caudally oriented femur, an incomplete fibula, and a laterally compressed pelvis (Fig. 1A–B). Type 1 bats are hypothesized to be poor walkers and include most of the family Phyllostomidae. Type 2 bats are characterized by a more laterally oriented femur, an incomplete fibula, and a more robust and less laterally compressed pelvis than Type 1 bats (Fig. 1C–D). These bats are hypothesized to be somewhat competent walkers and include the families Emballonuridae, Nycteridae, Natalidae, and Vespertilionidae. Type 3 bats are characterized by robust pelvis and limb bones, including a laterally oriented femur and laterally pointing feet, a complete fibula, and a robust pelvis with a large acetabulum (i.e., femur socket on the pelvis) (Fig. 1E–F). Type 3 bats are the most terrestrially competent, and include the family Molossidae, as well as vampire bats (Phyllostomidae: Desmodontinae) and *Mystacina*

(Mystacinidae); Type 3 bats, with few exceptions, have been the only bats studied with regards to their terrestrial competency.

Very little is known about bat trackmaking abilities and trackways, and no bat tracks or trackways have been identified in the rock record. No studies have been published on the trackway-making ability of any species of bat from a neoichnological perspective, in which track and trackway morphology are described in detail using constrained media consistency, videography, photography, and plaster casting of resultant traces. Only two attempts to study bat trackways have been published. Lawrence (1969) studied the terrestrial locomotion of three species of European vespertilionids (considered Type 2 bats by Vaughn [1970] and Schutt and Simmons [2006]) and used talc powder placed on top of soil to record tracks. The trackways produced were presented as stylized illustrations rather than actual photographs and/or line drawings of photographs. Dietz (1973) observed the terrestrial behavior of several molossids (Type 3), phyllostomids (Type 1), and vespertilionids (Type 2), using paper smoked with kerosene to record tracks and determine the variation between species and throughout ontogeny within a species; however, neither videos, photographs, nor illustrations of their behaviors, tracks, and trackways were published. Few bat studies using treadmills, force plates, high speed photography, and other methods to quantify gait types and terrestrial abilities have been conducted, mostly with Type 3 bat species known to exhibit high levels of terrestrial competency, such as the common vampire bat (*Desmodus rotundus*; Phyllostomidae: Desmodontinae), New Zealand short-tailed bat (*Mystacina tuberculata*; Mystacinidae), and the Bonda mastiff bat (*Molossus currentium*; Molossidae) (e.g., Altenbach, 1979; Riskin et al., 2005, 2006; Voigt et al., 2012). Those studies, however, did not focus on or illustrate any tracks and trackways.

The purpose of this paper is to present our neoichnological study of the locomotor behaviors and resulting traces of the Type 1, Neotropical fruit bat *Carollia perspicillata*. This study expands on the works of Lawrence (1969) and Dietz (1973), both of which demonstrated that Type 1 and Type 2 bats can produce tracks and trackways. Research presented here fills a gap in the knowledge of the terrestrial locomotion of presumed poor-walking Type 1 bats. Identification of extant bat tracks and trackways, regardless of locomotion type, would be useful as keys to identify them in the Cenozoic record and supplement the bat body-fossil record, resulting in a more complete history of bat evolution, distribution, and behaviors. The possible occurrence of bat trackways in the rock record, regardless of their terrestrial ability, may provide evidence to better understand their paleobiogeography and when bats became globally distributed.

BACKGROUND

Bats (order Chiroptera) are one of the most speciose and widespread mammal groups, with over 1,200 extant species occurring on every continent except Antarctica (Simmons, 2005). Bats have been historically subdivided into two suborders: (1) the Old World Megachiroptera, which consist of the nonecholocating flying foxes (Pteropodidae), and (2) the Microchiroptera, which have a worldwide distribution and have diversified into frugivores, insectivores, nectarivores, omnivores, carnivores, and sanguinivores (i.e., blood eaters). Molecular studies have cast doubt on the validity of these suborders, instead uniting the families Craseonycteridae, Hipposideridae, Rhinolophidae, Rhinopomatidae, and Megadermatidae with Pteropodidae to form the suborder Yinpterochiroptera, while assigning all other bats to the suborder Yangochiroptera (Van Den Bussche and Hoofer, 2004; Teeling et al., 2005). Recent analyses

incorporating molecular data group bats in the Laurasiatheria, a group of placental mammals that also includes Cetartiodactyla (even-toed ungulates and whales), Perissodactyla (odd-toed ungulates), Carnivora (e.g., cats, dogs, bears), Eulipotyphla (moles, shrews, hedgehogs, and solenodons), and Pholidota (pangolins) (Lin and Penny, 2001; Van Den Bussche and Hofer, 2004; Meredith et al., 2011; O’Leary et al., 2013). The time of divergence of bats from other laurasiatherians has been proposed to be between 70–89 million years ago, during the Late Cretaceous (Lin and Penny, 2001; Bininda-Emonds et al., 2007; but see O’Leary et al., 2013 for a hypothesized early Cenozoic origin), and the most recent common ancestor for extant bats is calculated to have lived ~64 million years ago, during the earliest Paleocene (Teeling et al., 2005).

The earliest bat body fossils are known from the Eocene of France, Australia, and Portugal (Hand et al., 1994; Tabuce et al., 2009), with the earliest potential pteropodid known from a single partial skeleton from the Oligocene of Italy (Meschinelli, 1903; Habersetzer and Storch, 1987), although the phylogenetic placement of this fossil has been disputed and it may belong to a more basal lineage (Schutt and Simmons, 1998). A single tooth from southern Thailand raises the possibility that pteropodids were present in the late Eocene (Ducrocq et al., 1992). No bat tracks or trackways have been found in the rock record.

Early Eocene bats appear almost simultaneously in Africa, Australia, Europe, India, North America, and South America (Hand et al., 1994; Tejedor et al., 2005; Smith et al., 2007; Tabuce et al., 2009; Ravel et al., 2011; Smith et al., 2012). At least 38 genera are known worldwide by the end of the Eocene (Eiting and Gunnell, 2009). The earliest bats known from postcranial material are remarkably similar to modern microchiropteran bats; *Icaronycteris index*, from the lower Eocene Green River Formation (Wyoming, USA), was until recently the

most primitive known bat. *Icaronycteris index*, however, exhibits numerous adaptations in the ear that indicate it could echolocate, suggesting they were almost certainly capable flyers (Jepsen, 1966; Simmons and Geisler, 1998). The discovery of *Onychonycteris finneyi*, also from the Green River Formation, represents the first well-preserved Eocene bat that was seemingly incapable of echolocating (e.g., cochlea more similar in size to modern nonecholocating bats). With five clawed digits on the forelimbs and differently proportioned forelimbs and hindlimbs than all other known fossil and extant bats (i.e., more similar to an arboreal nonflying mammal), this species represents the most primitive known among the Chiroptera (Simmons et al., 2008). Bats are, therefore, presumed to have arisen from arboreal, nonecholocating ancestors; however, no transitional forms between bats and their ancestors are known from the fossil record.

Carollia perspicillata is very well studied and is considered a model organism among bats (e.g., Heithaus and Fleming, 1978; Rasweiler and Badwaik, 1996; Oliveira et al., 2000; Sterbing, 2002; Chen et al., 2005; Cretkos et al., 2005; Brinkløv et al., 2011). These are frugivorous Neotropical bats within the family Phyllostomidae (the New World leaf-nosed bats) and the subfamily Carolliinae. *Carollia perspicillata* is the most widespread species of its genus, with a range extending from southern Mexico to southern Brazil (Hoffmann and Baker, 2003). Members of this genus occupy secondary forests to a greater degree than other frugivorous phyllostomids and are known to feed primarily on the fruit of *Piper* species (Heithaus and Fleming, 1978; Bonaccorso and Gush, 1987; Mello et al., 2004; Thies and Kalko, 2004). *Carollia perspicillata* is one of the largest of the genus in body size, occupies old-growth forests more frequently, and relies less on *Piper* fruit than co-occurring species; it also occupies a larger foraging range than congeners, including *C. castanea* and *C. sowelli* (originally reported as *C. brevicauda*; Fleming, 1991). Carolliines exhibit a cranial morphology intermediate between the

highly frugivorous stenodermatines and more insectivorous phyllostomids (York and Papes, 2007), and are presumed more variable in diet. *Carollia perspicillata* exhibits higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values in fur and fecal samples than other species of the genus, indicating a more varied diet with less reliance on insects than other *Carollia* species (York and Billings, 2009).

The pelvic and hindlimb morphology of *C. perspicillata* falls under the Type 1 grouping along with most other phyllostomids (Figs. 1A–B, 2). *Carollia perspicillata* is presumed to be a relatively poor walker, however, no studies of its walking abilities have been conducted, and very little work has been conducted on bats that are not already known to be terrestrially competent (with the exception of Dietz, 1973). *Carollia perspicillata* has, however, been reported to be caught with regularity in rodent traps (R.M. Timm, personal communication, 2015), possibly indicating a more significant terrestrial life history component than previously thought.

MATERIALS AND METHODS

Research was conducted using four individuals of *Carollia perspicillata* (Phyllostomidae: Carollinae) at the Lincoln Children's Zoo in Lincoln, Nebraska, on 19 January, 2012. The four bats used ranged in size from 17–21 g, with a mean mass of 18.75 g. Medium-grained sand (0.25–0.50 mm particle size) was placed in a 125 cm long by 25 cm wide by 6 cm deep tray. Moisture of the sand was measured by weighing a sample of sand while still wet and drying it in an oven overnight. After 24 hours the sample was weighed again. Percent moisture values on the sand ranged from 12–21%. A Plexiglas® cover was placed over the tray to prevent bats from flying. This cover measured 125 cm long by 25 cm wide by 21.5 cm tall. Three separate openings were cut into the top of the Plexiglas® and covered with removable lids to allow for

access to the tray to place and remove the bats (Fig. 3). The Plexiglas® cover was inverted for one bat that attempted to fly, reducing the space available above the sediment to <10 cm.

Each bat was placed individually into the experimental setup and its behavior documented with photography and digital video recordings. Video was analyzed by reducing the speed in order to accurately document the footfall patterns and other behaviors. The length of time an individual bat remained in the setup varied, but did not exceed 25 minutes. Bats were allowed time to acclimate to the experimental setup. They were removed from the setup when they stopped exploring the area and remained stationary for several minutes, including refusal to make more tracks by clinging to the wall of the tray, or when the sediment surface was sufficiently covered with tracks. Upon removal from the tray, the bat was returned to its exhibit. The resulting trackways were cast using Labstone® dental plaster (1.5:1 plaster to water ratio), and additional photographs of the plaster casts were taken. Novel measuring rubrics were developed from the resultant tracks and trackways recorded in the plaster casts (Fig. 4). When possible, track width and length, pace length, stride length, internal and external trackway width, angle of divarication from the midline, and angle of divarication from nearby tracks were measured from the plaster casts.

Locomotor behaviors were compared to those gaits designated by Hildebrand (1989) in studies on tetrapods. A gait refers to any regularly repeated terrestrial locomotor behavior, whereas a walk refers to any gait in which the limbs spend more than 50% of a stride in contact with the ground or, alternatively, a gait in which at least one limb touches the ground at all times. Symmetry refers to the placement of each limb of a pair being evenly spaced in time; asymmetry occurs when both limbs of a pair function simultaneously (Hildebrand, 1980, 1985, 1989;

Hutchinson et al., 2003). Locomotion behaviors observed in *C. perspicillata* not fitting into existing categories were described as new patterns of locomotion.

RESULTS

Locomotor Behaviors

Carollia perspicillata exhibited three different locomotor behaviors and one nonambulatory tracemaking behavior, designated as the diagonal sequence walk, breaststrokelike crawl, hop, and searching behavior. All behaviors except the hop were performed in the experimental setup by more than one bat, although several bats used the hop when taking to flight after being placed into their enclosure. Two casts were made of the walking trials (Figs. 5–6). Cast 1, 21% sediment moisture content in medium-grain sand, recorded every type of track morphology that was produced during the experiments. Cast 2, 12% sediment moisture content in medium-grain sand, recorded only claw imprints of the manus and a few possible pedal tracks. The only extensive trackway produced in the trials is preserved on Cast 1.

The most typical quadrupedal method of locomotion, observed in two bats, was a diagonal sequence walk with a left pes (LP), right manus (RM), right pes (RP), and left manus (LM) pattern (Fig. 7; Supplemental video 1). This behavior began with the LP as the most caudally extended limb. The LP was then lifted and placed more proximal to the body than the RP (Fig. 7A–B). Next, the RM was extended and placed roughly level with the head; the bat then pulled its body forward, resulting in the shoulder in a position near the RM (Fig. 7C–D). The RP, which had been extended the most caudally of any limb, was then picked up and placed proximal to the body (Fig. 7D–E). Next, the LM was brought forward and placed roughly level with the head, as the bat pulled its body into a position with the shoulder level with LM (Fig. 7F–H). At

this point, the RP was the most caudally extended limb and was next picked up and moved proximal to the body, which resulted in a similar position to that from which the bat began moving. In very few instances was this gait used for more than three consecutive strides, however, as the bat often switched to another locomotor behavior (see Supplemental video 1).

The breaststrokelike crawl resulted from the bat simultaneously extending forward both forelimbs, planting manus digit I into the sediment with the wrists approximately level with the head, and pulling the body forward with little or no assistance from the hindlimbs (Fig. 8; supplemental video 2). The bat pulled its body forward to the point that its wrists were level with, or just posterior to the shoulders (Fig. 8A–D). The forelimbs were then lifted and returned to a similar position with wrists level with the head (Fig. 8E–H). The bat repeated this pattern for as many 13 strides, but most ranged from four to nine strides before switching to another locomotor behavior or stopping. The resulting motions appeared similar to a swimmer performing the breaststroke.

A modification of the breaststrokelike crawl, termed here the one-armed crawl, was performed by one bat. This movement resulted from the bat extending only one forelimb forward and placing digit one in the sediment in a position with the wrist level with its head. The body was then pulled forward to the point that the wrist was level with the shoulder before the bat picked its forelimb up and extended it to begin the motion again (Fig. 9; supplemental video 3). Use of the other forelimb and hindlimbs during locomotion varied by stride. At least once the bat appeared to push off with its right forelimb as it pulled its body with the left forelimb. The feet were placed independently of each other to begin the movement: first the left hindlimb was placed proximal to the body and then the right, although both feet were moved in unison by the

final stride, as in the breaststrokelike crawl. The one-armed crawl was only performed by one bat for a single series of four strides.

The hop was an asymmetrical movement that involved the bat extending both forelimbs simultaneously as in the breaststrokelike crawl, but neither manus nor pedes were in contact with the medium before the forelimbs again made contact with the sediment. The forelimbs were used to propel the bat off the surface and move forward. The hop is similar in all other respects to the breaststrokelike crawl. The hop was only definitively observed in the video recordings once; there may have been several other instances but the video footage was obscured by the Plexiglas® (Fig. 10; Supplemental video 4).

A fourth behavior exhibited by the bats is termed the searching behavior. As the bat remained in place, one hindlimb was extended. At maximum hindlimb extension the toes were extended outward and placed onto the sediment surface. The digits were then contracted, gripping the sand, and the hindlimb pulled toward the body. This series of motions was continued for 2–5 times with the same hindlimb before performing the same motions with the other hindlimb (Fig. 11; Supplemental video 5). At no point were both hindlimbs in motion at the same time. The hindlimb was rarely extended into areas it had previously covered while performing the behavior. The searching behavior did not typically result in any forward or backward motion; however, the bat often rotated itself during this process, which resulted in the bat facing in a different direction from the one in which it began. When body rotation did occur, it was either clockwise or counterclockwise and ranged between $\sim 180^\circ$ and 360° .

Traces Recorded in Plaster Casts

Resulting traces apparent in casts of *Carollia perspicillata* trackways include individual manus and pes tracks as well as arcuate traces, clustered pedal traces (Fig. 12), and in one case an extensive trackway (Fig. 13). Manus tracks consist of only a single claw mark corresponding to the first digit (Figs. 12A, 13). These track shapes range from nearly circular with diameters of < 3 mm to elongated marks up to 23.4 mm long and 8.6 mm wide (Table 1). The longer axis is always oriented in the direction of locomotion. Manus tracks are present throughout both slabs and most are not obviously affiliated with a particular trackway.

Pedal tracks consist of four to five digit impressions 5.8–16.9 mm wide, with a mean of 13.1 mm, and 5.7–16.4 mm long, with a mean of 10.1 mm (Table 2; Figs. 12B–C, 14). Width of individual digit impressions within pedal tracks ranges from 1–1.5 mm. The widest, longest, and deepest pedal digit impression usually corresponds to digit 5. In cases where only four pedal digit impressions are preserved, digit one is absent. Pedal tracks most often occur in clusters of as few as two or as many as four to five sets of tracks, but may also be present as isolated tracks with no other associated tracks. Pedal tracks present in clusters may be overprinted, obscuring some individual tracks.

Arcuate traces correspond to the first digit on the manus and have widths from 2.07–3.74 mm (Table 3). These tracks range between 20.49–101.24 mm long, measured along a straight line drawn between the two ends, and 21–112 mm, measured along the arc (Table 3; Figs. 4C, 12D, 15).

Most bats did not perform continuous crawling behaviors long enough to leave a definitive trackway. Only one trackway was observed in the plaster casts (Fig. 13). The trackway is identifiable by a series of manus claw drags parallel or subparallel to the direction of locomotion averaging 79.9 mm apart, measured from the inner margin of the left track to the

inner margin of the right track at the closest point (see Fig. 4A). The tracks range from 61–88 mm apart. Individual manus tracks associated with the trackway range from 5.7–23.4 mm long, with a mean of 12.7 mm, and 2–8.6 mm wide, with a mean of 3.3 mm. No pes tracks are apparent in association with the trackway (see Table 1; Fig. 13).

DISCUSSION

Locomotor Behaviors

Of the locomotor behaviors described by Hildebrand (1989), only the diagonal sequence walk was performed by *Carollia perspicillata*. The use of a diagonal sequence walk—rather than the more commonly used lateral sequence gait (i.e., lateral sequence walk or run) in other tetrapods (Hildebrand, 1989)—may be a function of the force-generating forelimbs and relatively weak hindlimbs in bats (Howell and Pylka, 1977; Strickler, 1978), contrary to other tetrapods with more powerful hindlimbs (Coates et al., 2002). In a lateral sequence gait the manus that is placed on the ground immediately following a pedal footfall is on the same side of the body; in a diagonal sequence gait the manus that is placed on the ground immediately following a pedal footfall is on the opposite side of the body from that pes. Since most tetrapods have weaker or shorter forelimbs than hindlimbs (Coates et al., 2002), these definitions are applicable to tetrapod locomotion in many cases (Hildebrand, 1989). Bats, however, possess long, force-generating forelimbs and, in the case of *C. perspicillata*, the pes placed immediately following a manus footfall is on the same side of the body. While we have referred to this locomotor behavior as a diagonal sequence walk, it may also be considered a reverse lateral sequence walk if the initial point of reference is one of the forelimbs, rather than a hindlimb.

In addition to the diagonal sequence walk, previously undescribed locomotor behaviors observed in *C. perspicillata* include the breaststrokeline crawl and hop. The breaststrokeline crawl is defined as asymmetrical gait and the hop is defined as an asymmetrical movement following the criteria established by Hildebrand (1989). We formally define the breaststrokeline crawl as a gait in which the two forelimbs, placed near the head, are used to pull the bat forward with minimal to no assistance from the hindlimbs. The one-armed crawl is formally defined as a modified breaststrokeline gait in which only a single forelimb is used to pull the bat forward, with little to no assistance from either the hindlimbs or the other forelimb. The one-armed crawl functions like a hybrid between an asymmetrical and symmetrical gait; the pedes both contact the ground at roughly the same time, while the manus are staggered in time. The hop is formally defined as an asymmetrical movement in which the two forelimbs push the bat forward using a similar, breaststrokeline movement to the breaststrokeline crawl, with little to no assistance from the hindlimbs. Unlike the breaststrokeline crawl, however, the hop contains an aerial phase in which neither the manus nor pedes are in contact the ground. The hop was only observed to occur in *C. perspicillata* as a single movement and, therefore, cannot be called a gait; however, any sequence of repeated hops may be referred to as an asymmetrical gait. The hop may function to initiate flight from the ground, as we observed multiple bats using this behavior to take flight once they were released back into their enclosure. More research, however, is necessary to demonstrate the use and repetition of this behavior. The hop differs from the asymmetrical bound of *Desmodus rotundus* (Riskin and Hermanson, 2005; Riskin et al., 2006) in the range of motion exhibited by both the forelimbs and hindlimbs, and the more nearly simultaneous placement of the manus and pes in *Carollia*. We do not, however, rule out the possibility that the bound observed in *Desmodus* evolved from a phyllostomid behavior similar to the hop.

The lone nonambulatory trackmaking behavior also previously undescribed in *C. perspicillata* was the searching behavior. This behavior, which is likely similar to the one described by Dietz (1973) as searching, is the only one to consistently involve the pedes in track production that did not result in net movement of the bat; only rotational movement in the same spot.

The forelimbs of *C. perspicillata* are responsible for the majority of work done during locomotion. This is evidenced during the breaststrokelike crawl, where the hindlimbs are pulled behind with the rest of the body by the forelimbs, and by the absence of pedal tracks in association with the trackway preserved on Cast 1. There also appears to be minimal assistance from the hindlimbs in the diagonal sequence walk locomotion method.

Carollia perspicillata has not been observed to spend any time foraging or consuming food on the ground in the wild or captivity (Bonaccorso and Gush, 1987; Charles-Dominique, 1991), with the exception of those captured in rodent traps (R.M. Timm, personal communication). *Carollia perspicillata* is a ground-story (i.e., at the level of shrublike plants) frugivore that will select and remove fruit from the tree while hovering before taking it to a nearby roost to be consumed (Heithaus and Fleming, 1978; Bonaccorso and Gush, 1987; Charles-Dominique, 1991).

Dietz (1973) observed terrestrial behaviors by bats from three different families, including three genera of phyllostomids: *Artibeus*, *Leptonycteris*, and *Macrotus* (note that species were not given in that study). Dietz (1973) noted a loss of terrestrial ability within individuals of *Macrotus* and *Leptonycteris* after ~15 days of age. Juveniles of both genera displayed several different terrestrial abilities, including the searching behavior and variable and constant gaits. *Artibeus* performed only a searching behavior from adolescence to adulthood.

Dietz (1973) makes no mention of the breaststroke-like crawl, one-armed crawl, or hop in any of the phyllostomids observed.

Traces Recorded in Plaster Casts

Carollia perspicillata did not produce well-defined trackways in most cases. This is probably due to the occurrence of a Type 1 pelvic and limb morphology, which is not conducive for terrestrial locomotion (see Fig. 1–2). Dietz (1973) noted that in some bat species, including the phyllostomid *Leptonycteris*, juveniles were more terrestrially competent than adults. This may explain the incidence of a well-defined and extensive trackway in only one of the four bats studied; bats favoring the diagonal sequence walk may have been juveniles, although this was not confirmed. Since only one bat favored the diagonal sequence walk for more than a few strides, the preservation of a trackway on Cast 1 as opposed to Cast 2 was likely caused by the selection of particular bats and not the result of preservation bias as related to the percent moisture of the sand. Type 2 and Type 3 bats are more likely to produce consistent trackways based on their pelvic and limb morphology, and their tracks will probably be better represented and more easily recognized in the rock record.

Moisture content of the sand may result in differences in observed track morphologies, as has been demonstrated in other studies (e.g., Davis et al., 2007; Fairchild and Hasiotis, 2011; Schmerge et al., 2013). Only two levels of moisture were included in this study, and the cast with the higher percent moisture by volume (21%) preserved a wider range of track morphologies than did the cast of 12% moisture by volume.

Directionality of movement of the bat is evident in some preserved traces, such as those corresponding to the searching behavior, in which the pedal impressions converge in the cranial

direction in relation to the bat; and in the arcuate traces, which are convex in the cranial direction relative to the bat. Manus tracks always occur with the long axis parallel to the direction of locomotion. Due to their relatively uniform shape, however, manus tracks provide little other information about the direction of travel.

Implications for Identifying Tracks by Other Bat Species

Extant bats may end up on the ground for a number of reasons. Many species occasionally land on the ground to seek food and water and, therefore, may leave tracks and trackways similar to those produced by *Carollia perspicillata*. These include such bats as the omnivorous, shrewlike New Zealand short-tailed bat *Mystacina tuberculata*, which may have evolved terrestrial behavior due to the lack of ground-dwelling predators (Daniel, 1976, 1979), and gleaners (i.e., taking stationary prey from a surface, including the ground) of terrestrial prey, including the pallid bat *Antrozous pallidus* (Bell, 1982; Johnston and Fenton, 2001), northern long-eared bat *Myotis septentrionalis*, and the little brown bat *M. lucifugus* (Ratcliffe and Dawson, 2003). Greenhall (1968) noted that, in captivity, the false vampire bat (*Vampyrus spectrum*), the largest predatory bat in the world, will pounce on prey from above before crawling backward and up the walls of its enclosure to eat the prey item at its roost.

Dietz (1973) observed the terrestrial abilities of phyllostomids, molossids, and vespertilionids, and found that the phyllostomids—the most ecologically diverse bat family—were by far the least terrestrially competent. Of the seven bat genera observed, *Antrozous* was the most terrestrially competent and the two molossids, *Molossus* and *Tadarida* (species not given), appear to be competent walkers as well. These three bats may potentially produce well-developed and recognizable trackways. Only the phyllostomids *Artibeus*, *Leptonycteris*, and

Macrotus appeared to be poor walkers; they would likely produce trackways similar to those observed for *C. perspicillata*. Dietz (1973) also hypothesized that the change in terrestrial competency from juveniles to adults may be related to the need to avoid predators and to reach suitable takeoff locations, and the differing terrestrial competency among bats may be related to different ecological roles. Thus, juveniles of poor-walking species may make better-developed and recognizable tracks and trackways compared to adults.

Among phyllostomids, common vampire bats (*Desmodus rotundus*) have a unique suite of behaviors for acquiring food that includes occasionally approaching their prey from the ground and using a variety of terrestrial abilities, including running and hopping, to avoid being crushed by or to chase after their much larger prey, such as cattle and horses (e.g., Altenbach, 1979; Greenhall, 1988; Riskin et al., 2006). Vampire bats have also been observed drinking water from the ground, including lapping dew from grass (Greenhall et al., 1971). Altenbach (1979) hypothesized that the evolution of these terrestrial behaviors allow vampire bats to feed on small, terrestrial vertebrates and are secondarily advantageous for their sanguinivorous lifestyle. Vampire bats, therefore, could potentially produce well-developed and recognizable trackways, due to their greater degree of terrestrial competency. Although few bat species exhibit the levels of terrestrial competency of vampire bats, most, if not all bats possess hindlimb morphology capable of withstanding the mechanical stress of terrestrial locomotion (Riskin et al., 2005).

Candidates to Produce Tracks in the Rock Record

Extinct bats may possess a wider range of terrestrial ability and a larger terrestrial component of life history than previously thought. For example, Hand et al. (2009) argued that

the presence of *Mystacina*-like humeri from the Miocene Australian mystacinid *Icarops aenae* indicates that these bats were already competent terrestrial foragers in the early Miocene, long before their isolation in New Zealand.

The family Phyllostomidae, to which *Carollia* belongs, is hypothesized to include mostly poor walkers based on their Type 1 pelvic morphology, however, only one previous study has addressed the terrestrial ability of non-vampire phyllostomids. Some phyllostomids, such as *Vampyrum* and the vampire bats, exhibit varying degrees of terrestrial ability, and the earliest phyllostomids known from the fossil record include carnivorous bats similar to *Vampyrum* from the middle Miocene of Colombia (Savage, 1951; Czaplewski, 1997). In fact, the two species of *Notonycteris* known from the middle Miocene of Colombia have been placed within the monophyletic phyllostomid clade containing *Vampyrum*, *Chrotopterus*, and *Trachops*. Other phyllostomids are also known from these deposits and resemble such insectivorous species as *Tonatia* or *Lophostoma* and a species of glossophagine that represents the earliest known nectarivorous phyllostomid (Czaplewski et al., 2003). The most recent common ancestor of Phyllostomidae has been proposed to be as old as 42 Ma (Datzmann et al., 2010) or as young as 33.9 Ma (Baker et al., 2012). Baker et al. (2012) calculated that the diversification into the ecological niches now occupied by phyllostomids occurred between 29.5–18.5 Ma.

Desmodontine vampire bats (Type 3 morphology) have a wider distribution in the fossil record than modern *Desmodus rotundus*, which ranges from central Mexico to Uruguay and northern Argentina. At least three additional extinct species of *Desmodus* are recognized from the southern USA through northern Argentina to at least 600 km south of the current extent of *D. rotundus* (Morgan, 1988; Pardiñas and Tonni, 2000). Fossils place the earliest known members of this genus in the earliest Pleistocene of Florida, USA (Morgan et al., 1988; Morgan, 1991),

and a Pliocene or earlier origin for this group is likely. If sanguinivory evolved after terrestrial foraging in the ancestral desmodontine, as hypothesized by Altenbach (1979), then terrestrially competent vampire bats may date from more than 21 million years ago (early Miocene; Baker et al., 2012), before the divergence of *Diphylla*, the most basal living desmodontine.

Molossids, which possess the Type 3 pelvic and limb morphology like desmodontine and mystacinid bats, have a fossil record dating to the Eocene of Europe (*Cuvierimops parisiensis*) and North America (*Wallia scalopidens*) (Legendre, 1985). These bats may have been capable of well-coordinated gaits like their extant relatives (e.g., *Cheiromeles* and *Tadarida*) and are known from many fossil species worldwide belonging to both extant and extinct genera (e.g., Hand, 1990; Czaplewski, 1996; Arroyo-Cabrales et al., 2002; Morgan and Czaplewski, 2012).

Molecular data suggests that Molossidae may have diverged from other bat families very early in the Cenozoic, approximately 63 million years ago (Ammerman et al., 2012), and are some of the most likely candidates to leave traces in early Cenozoic deposits.

Tracks and trackways produced by members of the families discussed here may, therefore, have the potential to be identified in the geologic record as early as the early Eocene. Trackways produced by Type 1 phyllostomids may be present in deposits as early as the middle Miocene of South America, whereas those produced by Type 3 phyllostomids (the desmodontine vampire bats) may be expected to occur in deposits ranging anywhere from the Miocene to the Pleistocene of North, Central, and South America. The earliest potential tracks and trackways of Type 3 bats may be those produced by molossids in the Paleocene and may be cosmopolitan in distribution.

Several extinct families and genera from the early Eocene, including *Icaronycteris*, *Onychonycteris*, *Paleochiropteryx*, *Archaeonycteris*, and *Hassianycteris* are known from nearly

complete skeletons and some have been hypothesized to have gleaned prey from surfaces (i.e., stationary, rather than flying, prey) similar to modern bats that may be candidates to produce terrestrial traces (Simmons and Geisler, 1998; Simmons et al., 2008). Further study of the pelvis and limb morphology is necessary to better understand which of these extinct bats, if any, would have been more terrestrially competent than others.

Tracks and trackways produced by bats may be present in the fossil record dating to the late Cretaceous, based on hypothesized times of divergence from other laurasiatherians of up to 89 Ma (Lin and Penny, 2001; Bininda-Emonds, 2007; Meredith et al., 2011). Most molecular data indicates that bats were present by the Paleocene at the latest (Teeling et al., 2005; Ammerman et al., 2012), although a study by O’Leary et al. (2013) leaves open the possibility that bats did not arise until just after the Paleocene-Eocene boundary. The identification of tracks and trackways predating body fossils can be used to infer the presence of bats in early Cenozoic or latest Mesozoic deposits (see similar occurrences of zygodactyl [Lockley et al., 2007] and web-footed bird tracks [Lim et al., 2000], and early tetrapods [Niedźwiedzki et al., 2010; Narkiewicz and Narkiewicz, 2015]), as the earliest bats may be dentally indistinguishable from other early Cenozoic mammal groups (Hand et al., 2015). The identification of bat tracks and trackways may also provide insight into the dispersal of the earliest bats, which by the time of the first known body fossils are already largely cosmopolitan in distribution.

CONCLUSIONS

This is the first detailed study of the neoichnology of any species of bat, as well as the first to address the terrestrial ability of non-desmodontine phyllostomids. *Carollia perspicillata*, a bat with Type 1 pelvic and hindlimb morphology, produced distinctive manus tracks and pedal

searching traces associated with three different locomotor behaviors and one nonambulatory, trackmaking behavior. The breaststrokeliike crawl, including the one-armed crawl, and hop are newly defined behaviors for any bat species, whereas the diagonal sequence walk is known from other tetrapods, including bats. The nonambulatory searching behavior has previously been reported for other bat species. The diagonal sequence walk and the breaststrokeliike crawl were both used frequently and record abundant traces. Both methods of locomotion resulted primarily in elongate manus tracks but little to no associated pedal tracks. The one-armed crawl and hop were only each definitively observed once, and did not record obvious traces, but they would presumably leave traces similar to the breaststrokeliike crawl. Pedal tracks consist of four to five individual digit impressions and may occur as isolated tracks or as clusters. The searching behavior was the primary producer of pedal tracks, often in clusters of up to five individual tracks. The variability in terrestrial behaviors between individuals indicates that *C. perspicillata* may be more apt to exploit resources on the ground than previously thought.

Results of the locomotor behaviors and trackway-making ability of *Carollia perspicillata* suggest that Type 1 bat tracks and trackways may be readily identifiable in the rock record. The backward rotated hindlimbs in *C. perspicillata* and the caudally directed femur and hind feet results in the first digit of the hind foot being most lateral to the body. Manus tracks that are up to ten times as long as they are wide and oriented longitudinal to the trackway, coupled with pedal tracks that consist of four to five parallel claw marks, are indicative of *C. perspicillata* trackways. The occasional absence of digit one, and the prominence of digit five, may be useful in determining a chiropteran origin of tracks preserved in the rock record. Arcuate manus tracks and hindlimb searching traces may also be indicative of bat trackways produced by Type 1 bats

in the rock record. The preservation potential of bat tracks may vary with changing media consistency and this issue should be addressed with future research.

Type 2 and 3 bats are expected to vary in their locomotor behaviors due to their increased terrestrial competency compared to Type 1 bats. Juvenile bats with Type 1 pelvic and limb morphology, however, may be more likely than adults to produce consistent trackways in Type 1 bats, including such phyllostomids as *C. perspicillata*. This requires further testing, and future research should address the change in terrestrial ability throughout ontogeny. Trackways produced by Type 2 and 3 bats may have similar morphologies to Type 1 bats, but more neoichnologic work must be conducted to confirm any similarities and/or differences in locomotor behavior and track patterns. Manus tracks produced by Type 2 and 3 bats will probably resemble those produced by *C. perspicillata*, but pedal tracks will probably vary based on the more lateral orientation of the hindlimbs and feet in these bats. Type 2 and Type 3 bats would be expected to produce more extensive trackways and may be more readily identifiable in the rock record. A broader understanding of tracks and trackmaking ability of Type 1, 2, and 3 bats is needed to elucidate the impacts ecology, phylogeny, and morphology have on terrestrial behavior, and to clarify the potential behaviors of fossil bats. Future research will address the trackmaking ability of Type 2 and 3 bats, as well as bats from more varied ecological roles and phylogenetic relationships to better understand the terrestrial locomotor behaviors and trackmaking abilities of bats.

A thorough understanding of the breadth of terrestrial abilities performed by bats is needed. All three types of bat pelvic and limb morphologies must be studied to determine their relationship to terrestrial competency and range of tracks and trackways produced. Track morphologies of *Carollia* can be used in future neoichnological studies of bats with different

morphologies and ecological roles to establish synapomorphy-based criteria for the identification of bat tracks and trackways in the rock record. Bats have a Cenozoic fossil record dating to the early Eocene and a cosmopolitan distribution from the Eocene to the present. Modern bats occupy a wide variety of habitats and, while many are hypothesized to be poor walkers, a number of species are adept at terrestrial locomotion and may spend more time on the ground than is reported in the literature. A record of bat tracks and trackways in Cenozoic, and possibly latest Cretaceous deposits could supplement the bat body-fossil record, helping to shed light on the evolution and paleobiogeography of bats.

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FIGURE CAPTIONS

Figure 1—Three types of bat pelvic and hindlimb morphology. A) *Carollia perspicillata* (Phyllostomidae, Carollinae) pelvis KUNHM 76684. B) *Carollia perspicillata* hindlimb KUNHM 76684. C) *Eptesicus fuscus* (Vespertilionidae) pelvis KUNHM 11571. D) *Eptesicus fuscus* hindlimb KUNHM 11571. E) *Tadarida brasiliensis* (Molossidae) pelvis KUNHM 10896. F) *Tadarida brasiliensis* hindlimb KUNHM 10896. Scale bars are 1 cm.

Figure 2—Hindlimb morphology and orientation of living *Carollia perspicillata*.

Figure 3—Experimental setup.

Figure 4—Measuring rubrics for *Carollia perspicillata* traces. (A) Manus tracks and trackways. (B) Pedal tracks and searching traces. (C) Arcuate traces: a) manus track width, b) manus track length, c) pace length, d) stride length, e) minimum internal trackway width, e') maximum internal trackway width, f) minimum external trackway width, f') maximum internal trackway width, g) angle of divarication from trackway midline, h) width of individual pedal digit, i) length of individual pedal digit, j) width of single complete pedal track, k) angle of divarication of single pedal track, l) angle of divarication of pedal searching trace, m) width of arcuate trace, n) straight line distance of arcuate trace from tip to tip, o) maximum deviation of arc from n, p) internal trackway width, p') external trackway width, q) angle of arc.

Figure 5—*Carollia perspicillata* walking trial plaster Cast 1.

Figure 6—*Carollia perspicillata* walking trial plaster Cast 2.

Figure 7—Screen captures of video showing diagonal sequence walk locomotion method. A) Initial position with wrists approximately level with shoulders and feet at most distal point to body. B) Bat has brought left foot proximal to body. C) Bat places right wrist approximately level with head. D–E) Bat places right foot proximal to body. E) Bat places left wrist

approximately level with head. F–H) Body pulled forward to return wrists to a position level with shoulders and feet to a position distal to the body.

Figure 8—Screen captures of video showing breaststrokelike locomotion method. A) Initial position with both wrists level with head. B–D) Bat pulls body forward resulting in the position of the wrists level with the shoulders. E–G) Bat picks up arms and swings wings forward. H) Bat returns wrists to position level with the head.

Figure 9—Screen captures of video showing one-armed locomotion method. A) Initial position with left wrist approximately level with head, both feet distal to body, and right wrist behind shoulder. B) Bat pulls body forward with left arm, resulting in position of left wrist level with the shoulder. C) Bat picks up left foot and places it proximal to body. D–E) Bat picks up all limbs keeping only left forelimb in contact with sediment and moves body forward. F) Bat places left wrist approximately level with head. G–H) Bat repeats sequence, keeping left forelimb planted while moving the rest of the body forward.

Figure 10—Screen captures of video showing hop locomotion method. A) Initial position with left wrist slightly in front of head. B) Bat brings right forelimb forward, resulting in both wrists placed level with the head. C) Bat launches its body from the sediment, with both wrists as the only points of contact with the sediment. D) Bat picks both wrists up and swings them forward, no points of contact with the sediment. E–F) Bat lands with both wrists approximately level with the head.

Figure 11—Screen captures of video showing hindlimb searching behavior. A) Initial position with both feet proximal to body. B–C) Bat extends right foot and places it distal and slightly lateral to body. D–E) Bat extends right foot and places it distal and far lateral to body. F–H) Bat extends left foot and places it distal and medial to body.

Figure 12—*Carollia perspicillata* track morphologies. A) Individual manus imprints. B) Individual pedal trace. C) Pedal searching trace. D) Arcuate manus tracks.

Figure 13—*Carollia perspicillata* trackway on Cast 1 showing outlines of manus tracks.

Figure 14—*Carollia perspicillata* searching behavior trace on Cast 1 showing outlines of pedal tracks.

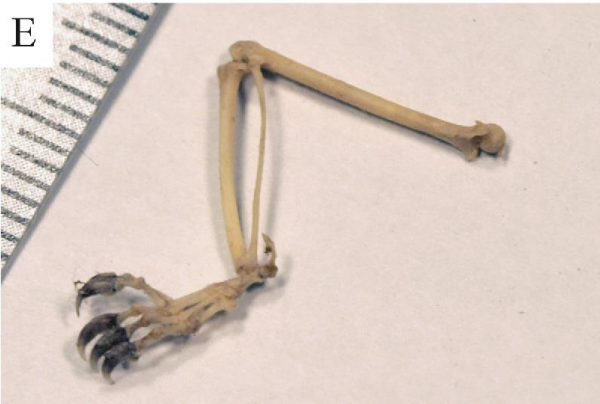
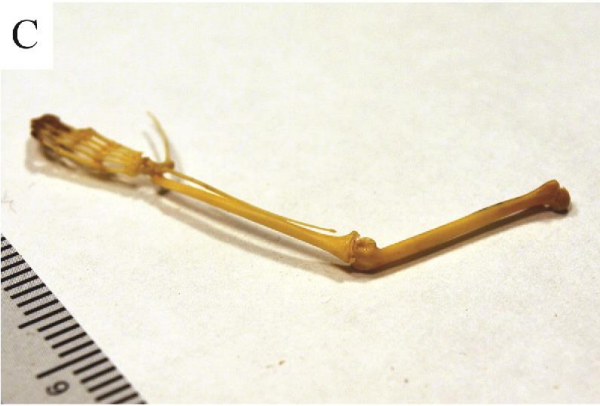
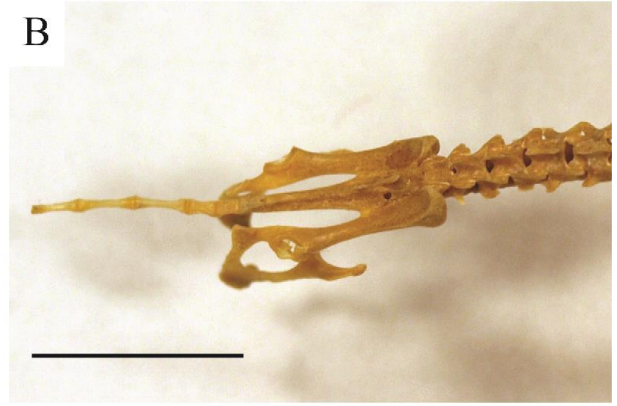
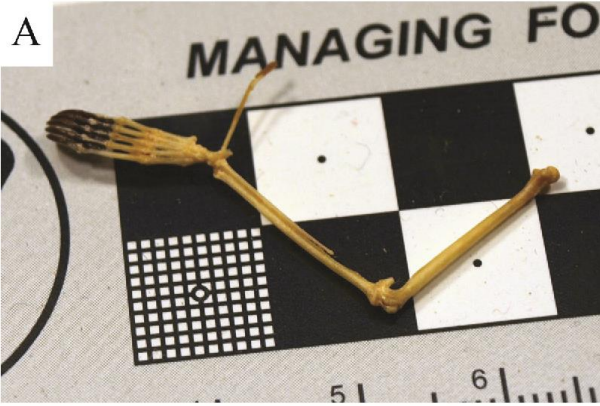
Figure 15—*Carollia perspicillata* arcuate manus tracks on Cast 1 showing outlines of arcuate tracks.

TABLE CAPTIONS

Table 1—Manus track measurements on Cast 1

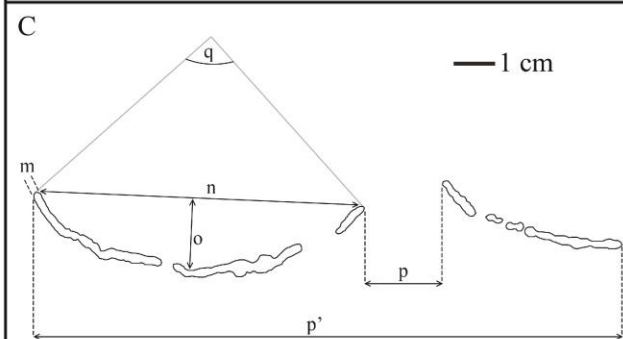
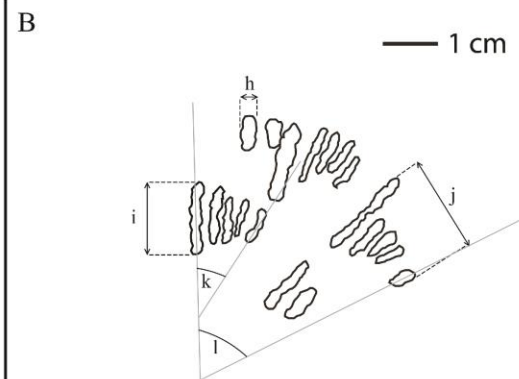
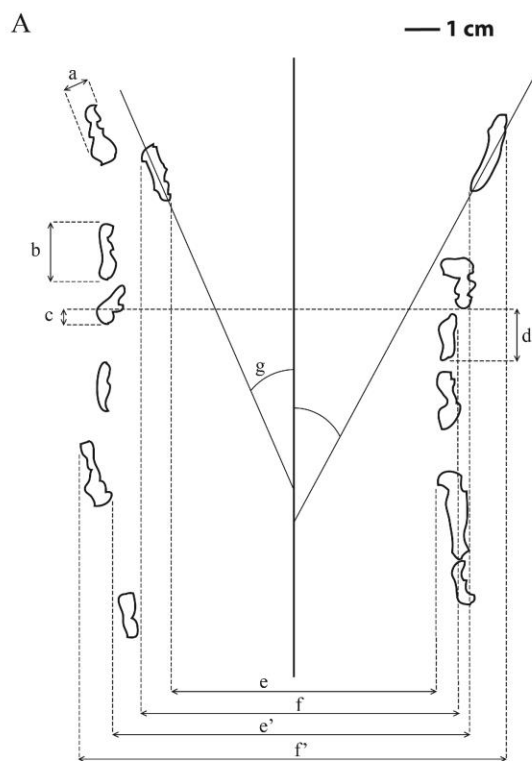
Table 2—Pes track measurements on Cast 1

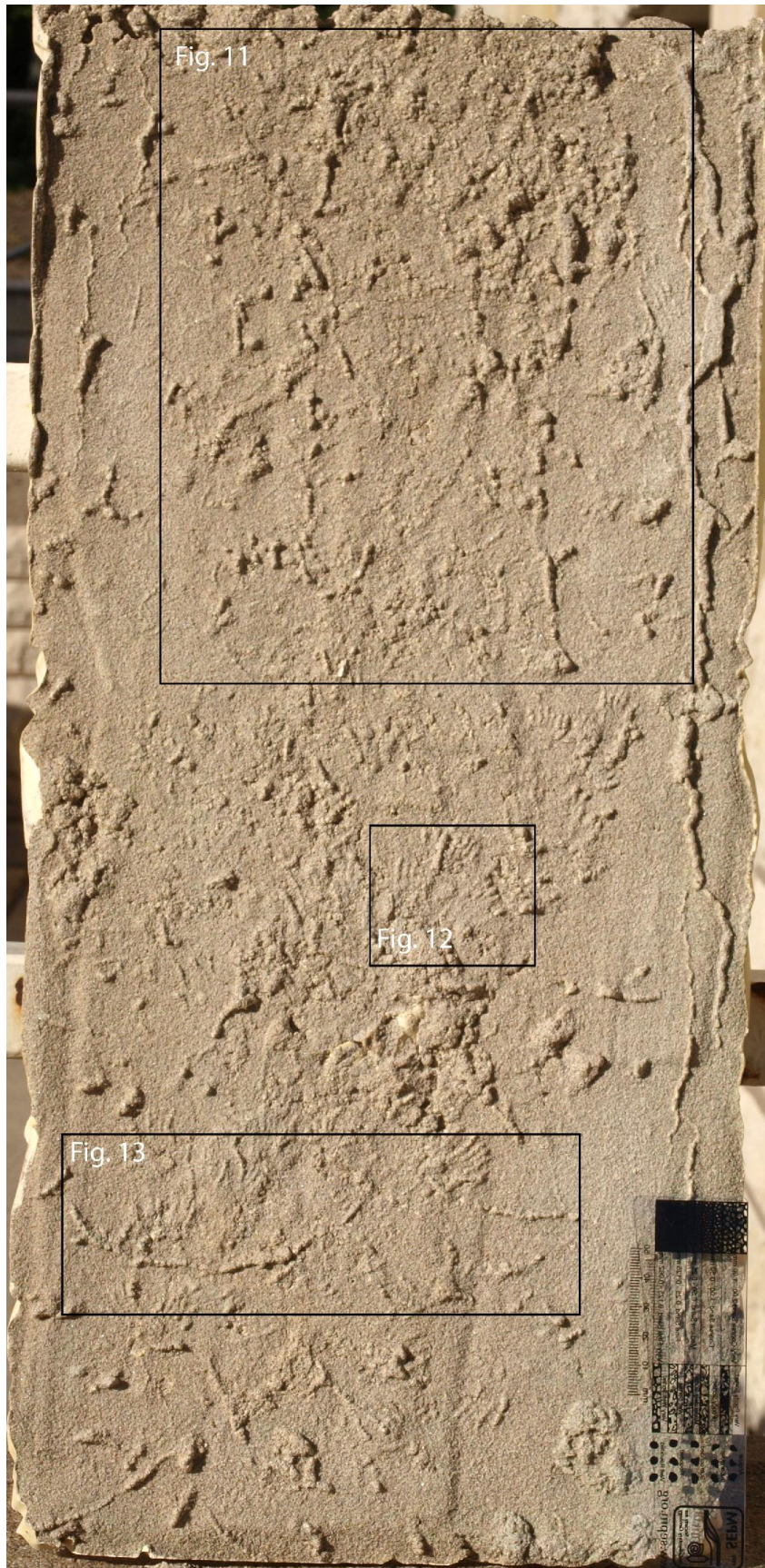
Table 3—Arcuate track measurements on Cast 1



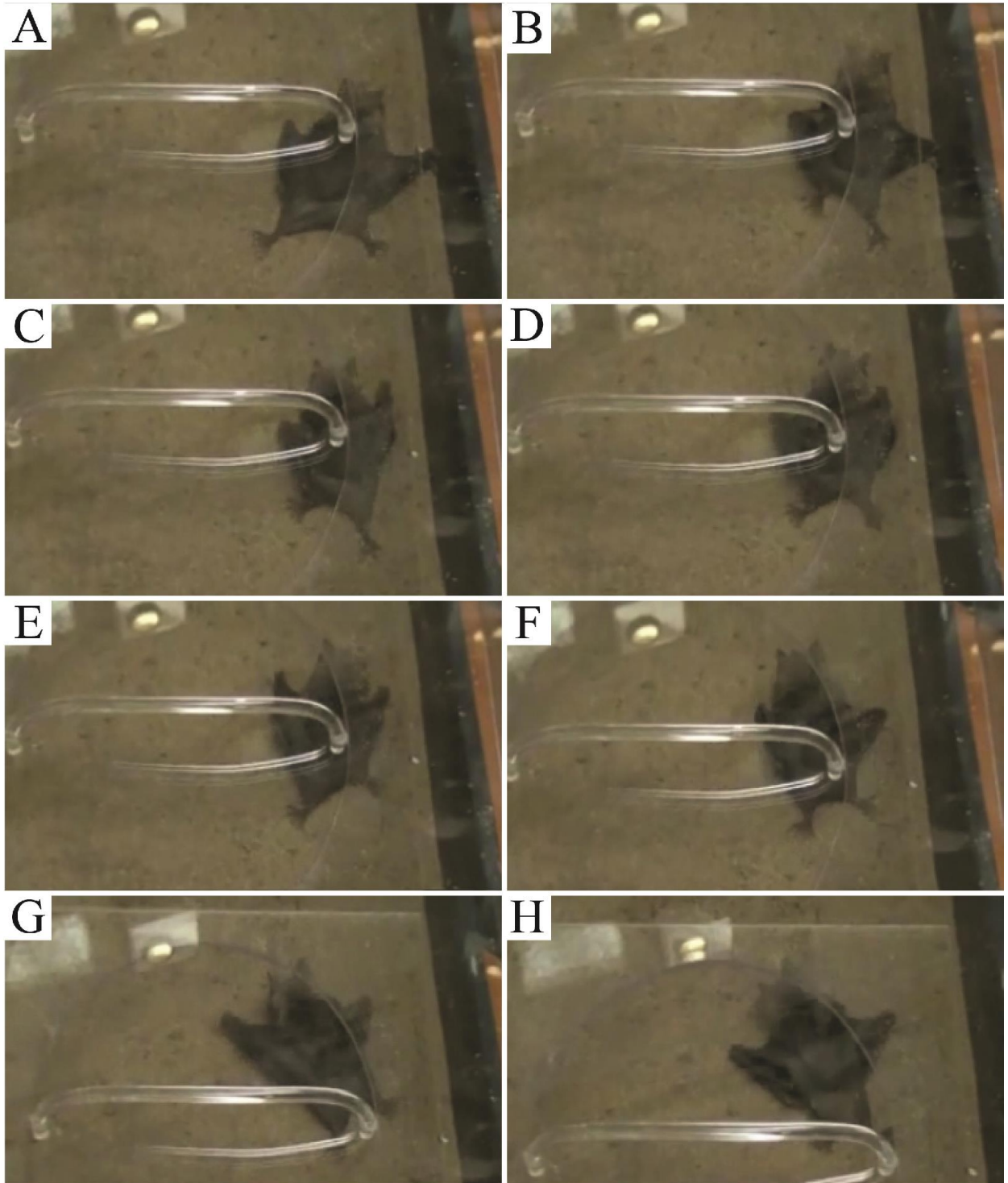












A



B



C



D



E



F

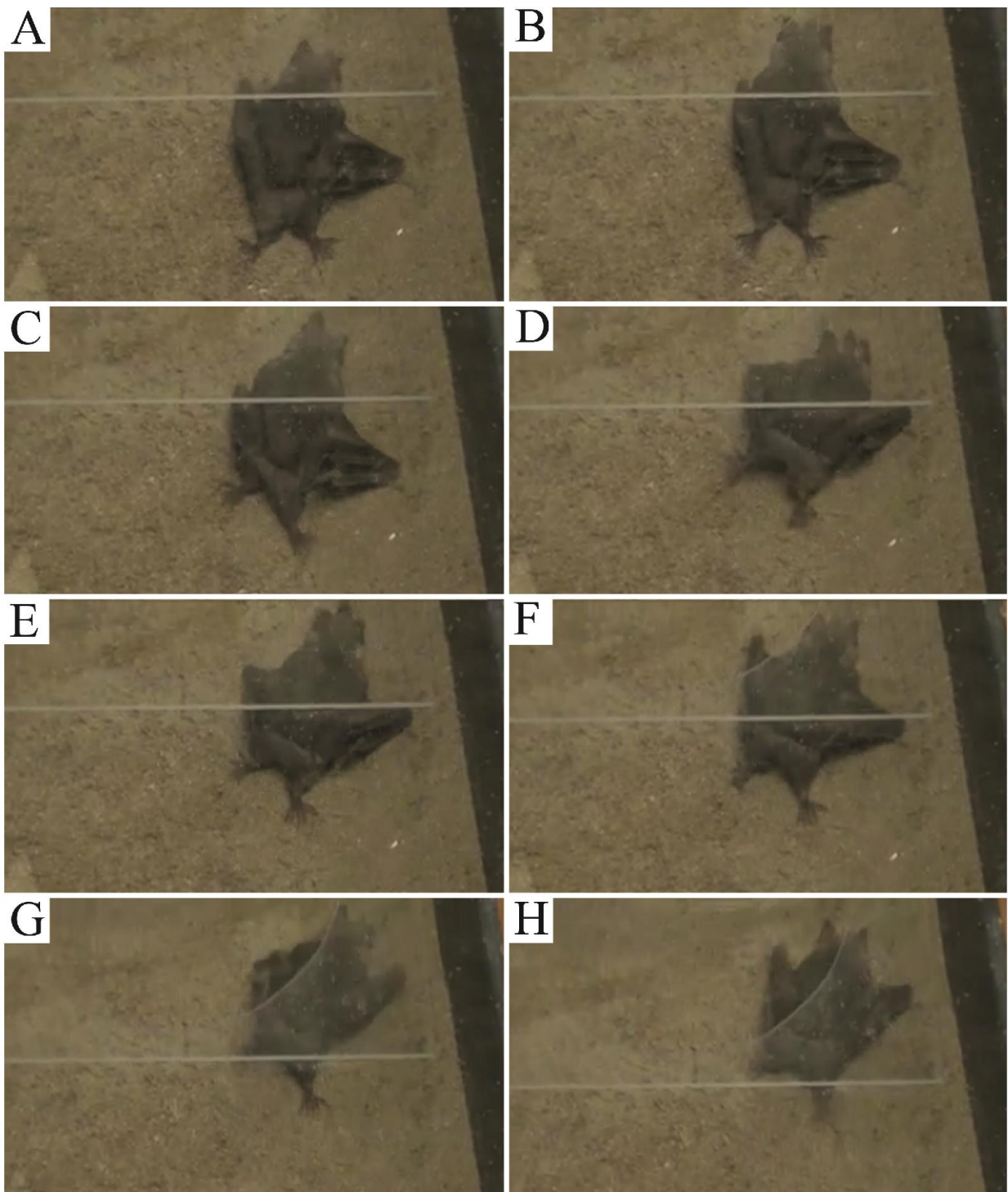


G



H





A



B



C



D



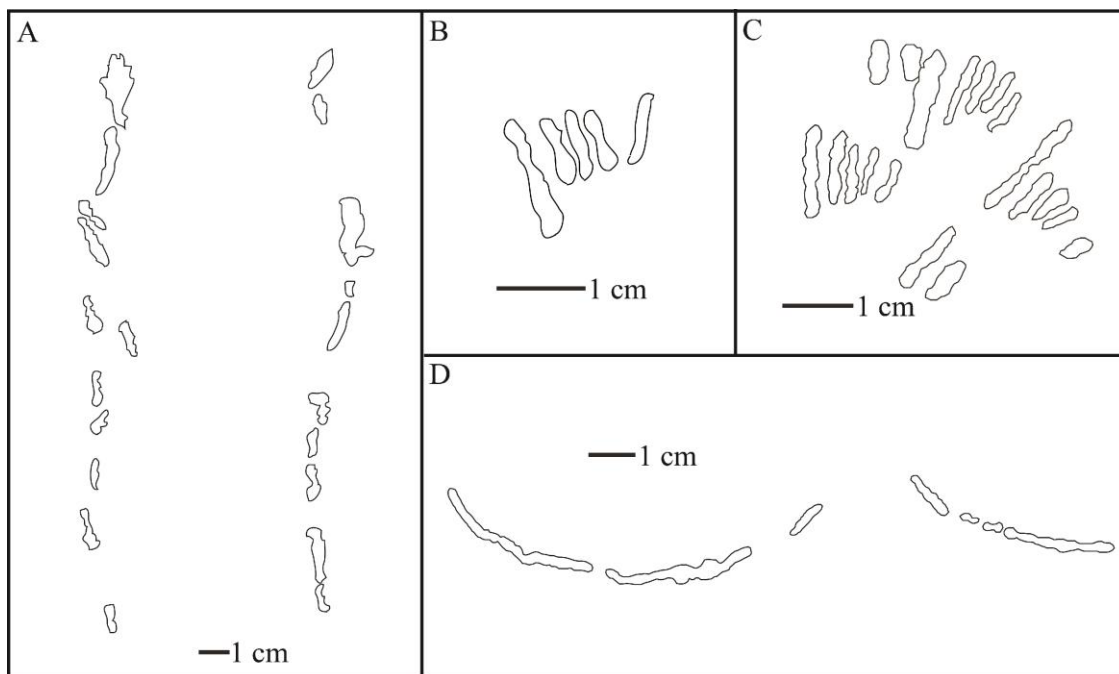
E



F

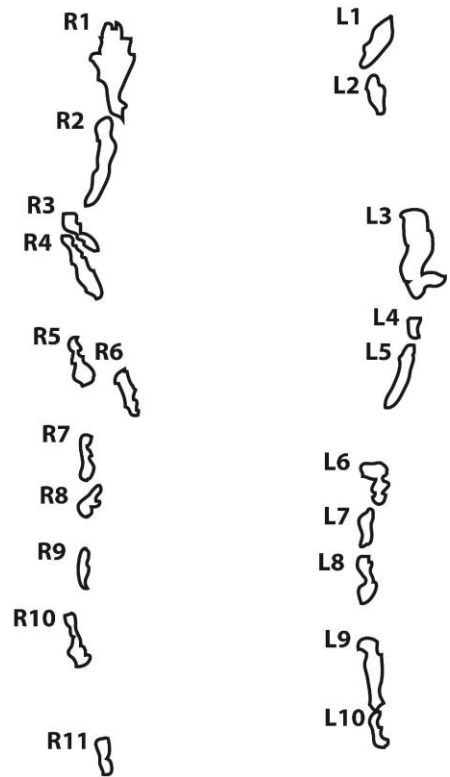


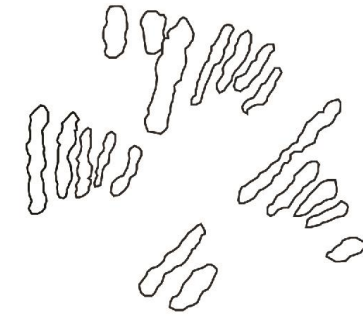
A**B****C****D****E****F****G****H**



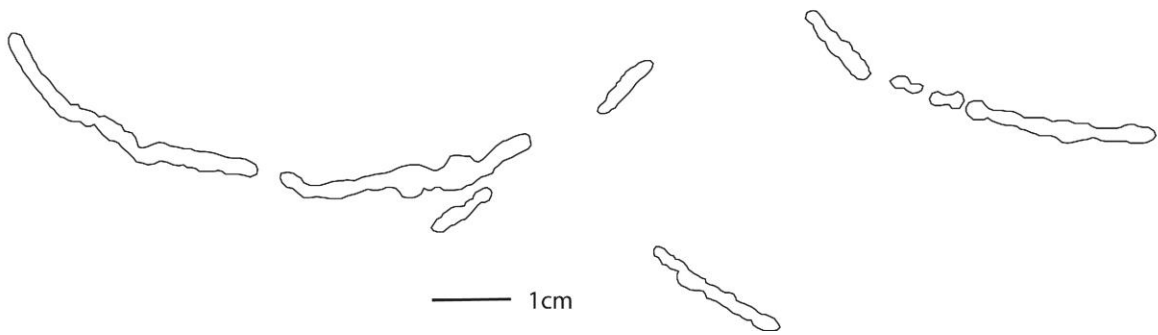


— 1 cm





— 1 cm



Location (top to bottom)	Length (long axis) in mm	Width (short axis) in mm
L1	19.5	8.6
L2	21.5	3.4
L3	12.4	2.3
L4	21.5	3.4
L5	12.6	2.9
L6	13.5	2.8
L7	12.5	3.4
L8	6.2	2.2
L9	9.9	2.4
L10	14.7	2.6
L11	9.7	2.4
L12	13.1	2.3
L13	7.7	2.5
L14	13.7	2.8
L15	9.9	3.4
L16	11.6	2
L17	13.9	2.6
R1	12.3	3.3
R2	7.9	3
R3	23.4	8
R4	5.7	2.5
R5	12.3	2.5
R6	11	4.2
R7	7.8	3.1
R8	11.2	3.6
R9	20.4	4.2
R10	7.9	2.4

Track/ Cluster	Number of tracks	Maximum length (mm)	Maximum width (mm)	Angle of divarication of single track	Angle of divarication of cluster
Pt01	1	8.4	15.6	35.79	N/A
Pt02	1	12.5	15.8	34.7	N/A
Pt03	1	9.6	9.8	2.48	N/A
Pt04	1	5.9	9.9	5.78	N/A
Pt05	1	12.2	16.6	33.45	N/A
Pt06	1	11.6	13	7.2	N/A
Pc01	4				77.75
Pc01-1	N/A	9.8	11.2	21.71	
Pc01-2	N/A			8.68	
Pc01-3	N/A	8.5	12.6	35.21	
Pc01-4	N/A	8.4	11.7	9.99	
Pc02	4				55.28
Pc02-1	N/A	9.3	13.9	25.63	
Pc02-2	N/A	5.7	5.8	7.72	
Pc02-3	N/A	13.4	13.6	15.7	
Pc02-4	N/A	16.4	15.2	11.06	
Pc03	2				36.57
Pc03-1	N/A	9.1	15.3	20.09	
Pc03-2	N/A	10	11	1.9	
Pc04	3				144.48
Pc04-1	N/A	9.1	16.6	67.29	
Pc04-2	N/A	10.5	13.9	7.9	
Pc04-3	N/A	8	12.8	14.22	
Pc05	3				37.43
Pc05-1	N/A	9.6	16.9	8.26	
Pc05-2	N/A	9.1	10.1	9.54	
Pc05-3	N/A	14.7	14.1	16.72	

Track	Length along arc (mm)	Straight line (mm)	Width (mm)
At01	112	101.24	3.74
At02	50	47.51	2.89
At03	21	20.49	3.02
At04	32.5	30.54	2.07
At05	66.5	62.16	3.61
At06	55	54.19	2.97
At07	24.5	24.14	2.49

**CHAPTER 3. TERRESTRIAL BEHAVIOR AND TRACKWAY MORPHOLOGY OF
NEOTROPICAL BATS IN THE FAMILIES PHYLLOSTOMIDAE AND
EMBALLONURIDAE**

Currently in review as:

Jones, M.F., and Hasiotis, S.T. Terrestrial Behavior and Trackway Morphology of Neotropical Bats in the Families Phyllostomidae and Emballonuridae: *Mammalian Biology*

ABSTRACT

Bats (Chiroptera) are unique among flying animals in being the only mammal capable of powered flight and the only extant group that is quadrupedal. Extant bats demonstrate varying levels of terrestrial competency, however, the terrestrial abilities of many groups are unknown. Here we examine the terrestrial ability and resultant traces produced by bats belonging to the families Phyllostomidae and Emballonuridae. Five different subfamilies of phyllostomids and the emballonurid *Saccopteryx bilineata* were analyzed for their terrestrial locomotor behaviors over a sand medium, with resultant tracks and trackways cast and measured. Behaviors and traces were compared to morphological criteria previously hypothesized to constrain terrestrial abilities of bats. Type 1 species (presumed poor walkers) performed only a breaststrokelike crawl and nonambulatory searching behavior, whereas the terrestrially adept Type 3 *Desmodus rotundus* performed a diagonal sequence walk and bound. Behaviors and traces produced by the intermediate Type 2 *S. bilineata* were indistinguishable from those of the Type 1 bats. Results only partially support the hypothesized morphological basis for terrestrial ability in bats and indicate that ecological differences or as yet unrecognized morphological variations may be the

cause of behavioral variations in bats of the same morphotype. This research fills gaps in our knowledge of the terrestrial behaviors of nondesmodontine phyllostomid bats, and is the first study to examine the terrestrial behaviors of any species of emballonurid.

INTRODUCTION

Modern bats exhibit a wide range of terrestrial abilities and some species, such as the New Zealand short-tailed bat (*Mystacina tuberculata*) and the common vampire bat (*Desmodus rotundus*), are very terrestrially adept (e.g., Altenbach, 1979; Daniel, 1979; Riskin et al., 2005, 2006; Schutt and Simmons, 2006). The pelvic and hindlimb morphology of bats may indicate a wider range of terrestrial abilities than is reported in the literature. Vaughan (1970) and Schutt and Simmons (2006) grouped bats into three categories based on their pelvic and hindlimb morphologies and presumed influence on their terrestrial ability (Table 1). Type 1 bats, which include most phyllostomids (New World leaf-nosed bats), possess a laterally flattened pelvis, a proximally incomplete fibula, and a posteriorly (i.e., caudally) oriented acetabulum. Type 2 bats, which include the emballonurids, as well as the vespertilionids, nycterids, and natalids, possess a slightly more robust pelvis, an incomplete fibula, and an acetabulum that is oriented more laterally than in Type 1 bats. Type 3 bats, which include the molossids, the desmodontine vampire bats (Phyllostomidae), and the New Zealand short-tailed bat, have a robust pelvis, a complete fibula, and a large, laterally oriented acetabulum. Types 1–3 bats are hypothesized to have increasing levels of terrestrial competency, in which species with large pelvises, complete fibulae, and laterally oriented hindlimbs are more terrestrially adept than those with laterally

compressed pelves and caudally oriented hindlimbs (Vaughan, 1970; Schutt and Simmons, 2006).

This study examines the terrestrial abilities and resultant traces (i.e., track and trackway morphologies) of nine species of Neotropical bats belonging to the families Phyllostomidae and Emballonuridae captured at Reserva Ecológica Bijagual de Sarapiquí (REBS) in the Caribbean lowlands of northeastern Costa Rica. Representatives from all five Costa Rican subfamilies of Phyllostomidae were used, as well as two individuals of the emballonurid *Saccopteryx bilineata* (greater sac-winged bat). The objectives of this research are to: 1) test the hypothesis that there is a difference in terrestrial ability between bats of Type 1, 2, and 3 pelvic and hindlimb morphology; 2) determine if behaviors observed are identical to those observed by Lawrence (1969), Dietz (1973), Riskin et al. (2006), and Jones and Hasiotis (in review), for other bat species; and 3) establish if there is a difference in terrestrial ability based on the ecological niche and/or feeding habit occupied by the bat.

Results of this research will be used to establish a database of bat track and trackway morphologies and terrestrial behaviors to identify possible bat traces in Cenozoic and potentially latest Mesozoic sedimentary deposits. Few studies have been conducted on the track-making ability and track and trackway morphology of modern bats (Lawrence, 1969; Dietz, 1973; Jones and Hasiotis, in review); the track morphology of bats that would be preserved in the geologic record is unknown. No trace fossils of bats are currently recognized, despite the identification of trace fossils from all other groups of animals capable of powered flight (e.g., Hasiotis, 2002; Kim et al., 2006; Lockley et al., 2008). A better understanding of the terrestrial behaviors and trackway morphologies produced by bats will allow for their identification in the fossil record,

resulting in a more complete understanding of bat evolution, behavior, and their global dispersal patterns.

BACKGROUND

Bats (Chiroptera) have a body fossil record extending to the early Eocene Epoch, ~54–56 Ma (Hand et al., 1994; Tabuce et al., 2009). Well-preserved bat fossils, such as *Icaronycteris index* and *Onychonycteris finneyi* from the lower Eocene Green River Formation of Wyoming, USA, indicate that primitive bats were already capable flyers (Jepsen, 1966; Simmons et al., 2008). *Onychonycteris* is the most primitive bat known from relatively complete skeletal material and may not have been capable of echo-locating (Simmons et al., 2008). Despite this and the presence of claws on all five digits of the hand, *Onychonycteris* is clearly recognizable as a bat, and does not represent a more basal transitional form. Other early Eocene bat fossils are known from Africa, Australia, Europe, India, and South America (Jepsen, 1966; Hand et al., 1994; Tejedor et al., 2005; Smith et al., 2007; Simmons et al., 2008; Tabuce et al., 2009; Ravel et al., 2011), indicating a relatively rapid global dispersal during the early Cenozoic. The lack of Paleocene body fossils, however, prevents a more detailed understanding of chiropteran dispersal patterns early in their evolution. Molecular studies estimate the time of divergence for all modern groups of bats to have occurred between 75–55 Ma, during the latest Cretaceous to early Paleogene periods, and bats are hypothesized to have split from the next most closely related mammal groups as early as 89 Ma during the Late Cretaceous Period (Bininda-Emonds et al., 2007; Meredith et al., 2011; O’Leary et al., 2013).

The family Phyllostomidae is arguably one of the most diverse among all mammals, and is the third most species-rich family within the Chiroptera (Wilson and Reeder, 2005). Five or

six subfamilies (depending on the placement of Lonchophyllinae) of Phyllostomidae are known from Costa Rica (Timm and LaVal, 1998), which generally divide along ecological niches (Ferrarezzi and Gimenez, 1996). The Stenodermatinae are largely canopy frugivores specializing on the fruits of such plants as *Ficus* and *Cecropia* (Bonaccorso and Gush, 1987; Charles-Dominique and Cockle, 2001). The Carolliinae are intermediate frugivores and insectivores, feeding on fruits of early successional plants, as well as supplementing their diets with a significant amount of insects (Bonaccorso and Gush, 1987; Thies and Kalko, 2004; York and Papes, 2007). The Glossophaginae, which previously also included the now recognized subfamily Lonchophyllinae (e.g., Wetterer et al., 2000; Baker et al., 2003; Parlos et al., 2014), are mostly nectarivorous, although some will occasionally supplement their diet with fruit and insects (Koopman, 1981; Godínez-Alvarez and Valiente-Banuet, 2000; Zortéa, 2003). The Phyllostominae are omnivorous to carnivorous, with many smaller species feeding mainly on insects, whereas some larger species will consume such small vertebrates as frogs, lizards, birds, and other bats (Gardner, 1977; Bonato et al., 2004). The three species belonging to the Desmodontinae are the only sanguinivorous bats, with *Desmodus rotundus* feeding primarily on mammal blood and *Diaemus youngi* and *Diphylla ecaudata* feeding mostly on the blood of birds (Greenhall, 1988).

The family Emballonuridae is found in the tropics and subtropics of both the eastern and western hemispheres and are commonly known as sheath-tailed bats, sac-winged bats (in the western hemisphere), or tomb bats (in the eastern hemisphere). Eight genera are known from Costa Rica (Timm and LaVal, 1998), all insectivorous. *Saccopteryx bilineata* is one of the best-studied emballonurids and is known to roost communally in harems of up to 50 individuals in buttress cavities of trees or on the sides of buildings (Bradbury and Emmons, 1974). *Saccopteryx*

bilineata is an opportunistic forager, occupying different habitats during times of peak insect abundance, feeding primarily on flies (Diptera) and beetles (Coleoptera). *Saccopteryx bilineata* typically forages for insects on the wing (i.e., hawking), roughly 3–8 m in the air (Bradbury and Vehrencamp, 1976).

Although terrestrial behaviors of the vampire bats, most notably *Desmodus rotundus*, have been extensively studied (e.g., Altenbach, 1979; Riskin and Hermanson, 2005; Riskin et al., 2006; Schutt and Simmons, 2006), very little work has been done on the terrestrial locomotion of nondesmodontine phyllostomids (Dietz, 1973; Jones and Hasiotis, in review), and no work has been done on terrestrial locomotion in emballonurids. The ecological diversity of the Phyllostomidae and the large biogeographic distribution of the Emballonuridae make both families ideal candidates to study the variability of terrestrial behaviors within Chiroptera.

MATERIALS AND METHODS

Research was conducted at REBS (10°21'N, 84°06'W; 300 m elevation) during early summer 2014. Seventy-four bats representing 12 species were caught over the span of 12 days, from 27 June to 8 July. Of these, nine species were selected, based on representation of multiple families and subfamilies: Seba's short-tailed bat, *Carollia perspicillata* (n=1); Sowell's short-tailed bat, *C. sowelli* (n=1); the pygmy fruit-eating bat, *Dermanura phaeotis* (n=1); the great fruit-eating bat, *Artibeus lituratus* (n=1); the common vampire bat, *Desmodus rotundus* (n=4); the common big-eared bat, *Micronycteris microtis* (n=1); Tomes's sword-nosed bat, *Lonchorhina aurita* (n=1); Underwood's long-tongued bat, *Hylonycteris underwoodi* (n=1); and the greater sac-winged bat, *Saccopteryx bilineata* (n=2) (Table 2). All species were captured in mist nets between 19:00–22:00, with the exception of the two *Saccopteryx bilineata*, which were

captured roosting during late afternoon on the walls of the REBS administrative building using a hand net. All bats were handled in accordance with permits issued by the Ministry of Environment, Energy, and Technology of Costa Rica and under protocols approved by the University of Kansas Institutional Animal Care and Use Committee.

Reptilite™ calcium carbonate sand (medium grain size, 0.25–0.50 mm) was placed in a tray with dimensions 52 x 25 cm to a depth of ~1 cm. Water was added to the sand, and a sample was weighed in order to determine the percent moisture (Table 3). The sample was placed in an oven, and after 24 hours was weighed again. Percent moisture values of the sand ranged from 4–11% for all but *C. perspicillata* (0%). For most experimental runs, a Plexiglas® sheet was placed directly atop the tray to prevent escape by the bat. A custom-built Plexiglas® and PVC lid was placed atop the tray for the larger bat species (*Desmodus rotundus* and *Artibeus lituratus*), raising the total height of the enclosure to 12.5 cm (Figure 1).

Bats were placed into the experimental setup after they were weighed, sexed, and forearm length measured (e.g., Timm and LaVal, 1998; Srinivasulu et al., 2010; Patterson and Webala, 2012). Bats were left in the experimental setup until they had sufficiently covered the sediment surface with traces or stopped moving and remained stationary for several minutes. The time individual bats spent in the experimental setup varied but did not exceed 25 minutes for any bat. Behaviors of the bats were documented with photographs and digital video recordings. Upon completion of a trial, the Plexiglas® lid was removed and the bat was allowed to fly away. Resulting tracks and trackways were cast with Labstone® dental plaster (2:1 plaster to water ratio).

Behaviors observed were compared to those noted by Riskin et al. (2006) for *Desmodus rotundus*, Jones and Hasiotis (in review) for *Carollia perspicillata*, Lawrence (1969) for three

species of European vespertilionids, and Dietz (1973) for several species of phyllostomid, molossid, and vespertilionids (Table 4). Other terrestrial behaviors were compared to those described by Hildebrand (1985, 1989) for nonchiropteran tetrapods.

RESULTS

Locomotor behaviors

Desmodus rotundus favored the bound defined by Riskin and Hermanson (2005), although some individuals also rarely performed a diagonal sequence walk. Most other phyllostomids and *Saccopteryx bilineata* favored the breaststrokelike crawl (Jones and Hasiotis, in review). Many of these bats also performed the nonambulatory searching behavior with their hind feet (cf. Dietz, 1973; Jones and Hasiotis, in review).

The bound performed by *Desmodus* is an asymmetrical gait as defined by Hildebrand (1985) in that both forelimbs strike the ground simultaneously rather than evenly spaced in time. To begin this movement, both forelimbs were brought forward so that the wrists and thumbs were positioned anterior to the tip of the snout (Fig 2A). The bat next placed its wrists and thumbs into the sediment and propelled its body forward (Fig 2B, C). During this phase, the hindlimbs were raised and brought proximal to the body. Before the bat landed, it swung its forearms forward into the starting position (Fig 2D), resulting in an aerial phase in which neither the hindlimbs nor the forelimbs were in contact with the sediment surface. The end of the stride resulted in a position with both wrists anterior to the tip of the snout and hindlimbs proximal to the body (Fig 2E), similar to the original position (Fig 2F; supplemental video SV1). The bound exhibited by *Desmodus* included two variations on hindlimb movement: hindlimbs in unison (i.e., both pedes struck the ground nearly simultaneously) and hindlimbs staggered (i.e., one pes

struck the ground before the other). During the bound, *Desmodus* positioned its wrists next to the body and directly under the elbows while folding the rest of the hand tightly next to the body. The entire body was held off the ground by both the fore- and hindlimbs.

Desmodus less frequently performed a diagonal sequence walk, a symmetrical gait in which each limb was moved independently of the other of the pair (Fig 3). To begin this movement, first the left manus was brought from a position with the wrist posterior to the head and placed with the wrist anterior to or level with the head (Fig 3A–C). Next, the right manus was similarly moved into a position with the wrist level with or anterior to the head (Fig 3D). The left pes was then raised and moved proximal to the body (Fig 3E, F). Finally the right pes was raised and moved proximal to the body as the bat moved its entire body forward, resulting in a position similar to when it began the stride (Figure 3G, H; supplemental video SV2). Occasionally, before the left pes had finished its movement the right pes was also raised and moved, resulting in a staggered hop with the hindlimbs.

The most frequent behavior performed by the nondesmodontine phyllostomids and *Saccopteryx* was the breaststrokelike crawl (Jones and Hasiotis, in review). This behavior began with the forearms outstretched and digit I roughly level with the eyes (Fig 4A). Both forearms were pressed onto the sediment and used to propel the body forward, resulting in a position in which digit I was level with the shoulders (Fig 4B). Once the body came to a stop, the bat swung both forelimbs forward simultaneously, returning to the starting position with digit I level with the eyes (Figure 4C–F; supplemental videos SV3, SV4). Hindlimbs were not involved in generating forward movement during the breaststrokelike crawl and were pulled along with the rest of the body by the forelimbs. During this behavior most of the body remained in contact with the sediment, and rarely, if ever, was the bat completely airborne. The breaststrokelike crawl was

performed by *Carollia perspicillata*, *C. sowelli*, *Dermanura phaeotis*, *Hylonycteris underwoodi*, *Lonchorhina aurita*, *Micronycteris microtis*, and *Saccopteryx bilineata*.

The searching behavior (Fig 5) has been described by both Dietz (1973) and Jones and Hasiotis (in review). This behavior started with the bat positioned with both hindlimbs outstretched (Fig 5A). First the bat gripped the sand with the toes of one foot while the other foot remained stationary. As the sand was grasped, the foot was pulled toward the body before being released (Fig 5B). The same hindlimb was extended and the motion began again (Fig 5C). Often the bat would switch between searching with both feet (Fig 5D–H), but only very rarely were both feet in motion at the same time (supplemental videos SV5, SV6). During the searching behavior the wings were either extended or retracted. Very little directional movement was observed during the searching behavior, but rotational movement of up to 180° was observed with regularity. The searching behavior was performed by *Artibeus lituratus*, *Carollia perspicillata*, *C. sowelli*, *Dermanura phaeotis*, *Lonchorhina aurita*, and *Saccopteryx bilineata*; although *A. lituratus* and *C. sowelli* only performed the behavior while clinging to the side of the experimental setup and not on the sand.

Traces recorded in plaster casts

The type and morphology of traces recorded in the plaster casts varied between species. *Desmodus* produced manus and pes tracks that often comprised extensive trackways (Figure 6). Manus tracks produced by *Desmodus* are robust, with a mean width of 7.7 mm and a mean length of 17.7 mm (Table 4), and may alternately preserve only the impression of digit I, only the impression of the wrist and distal forearm, or both types of impressions. In manus tracks that preserve both digit I and the wrist and distal forearm, digit I is identified as a thin impression

projecting at a $\sim 90^\circ$ angle from the more robust wrist impression, resulting in an L shape (Figure 7A). Manus tracks may be oriented with the long axis either parallel or perpendicular to the midline of the trackway. *Desmodus* pes tracks generally consist of the impressions of four to five individual pedal digits (Figure 7B), although in some cases as few as three were preserved. Pedal tracks are usually oriented with the long axes of the individual digits perpendicular to the trackway midline, although in some instances the long axes are parallel. The mean width of *Desmodus* pes tracks is 17.1 mm and the mean length is 11.4 mm (Table 5). Manus tracks were more abundant and deeper than pes tracks in casts of *Desmodus* trackways. Pes tracks were not observed in clusters in any of the *Desmodus* trackway casts. Trackways produced by *Desmodus* consist of both the individual manus and pes tracks, with the manus tracks being more abundant. Pes tracks, when present, occur closer to the trackway midline than do manus tracks, however, pes tracks are often not in close association with the manus tracks. Both manus tracks and pes tracks on either side of the midline appear as pairs that are roughly aligned in most trackways (see Figure 6).

No other bat species produced such distinctive traces as *Desmodus*, however, manus tracks produced by the other bat species were clearly recorded in most casts, and pes tracks were also occasionally present. Arcuate lineations were produced by *A. lituratus*, *C. perspicillata*, *C. sowelli*, *Da. phaeotis*, *L. aurita*, *M. microtis*, and *S. bilineata*. No other bat species produced manus tracks that were as robust as *Desmodus*, and very few preserved impressions of both digit I and the wrist and distal forearm.

None of the nondesmodontine phyllostomids produced recognizable trackways, nor did *Saccopteryx*. Casts of the tracks produced from these trials feature numerous manus tracks—evidenced by a $> 2:1$ length to width ratio—that are not noticeably aligned with respect to other

manus tracks or with pes tracks (Figure 8). In most cases, manus tracks do not preserve evidence of both digit I and the wrist and distal forearm, resulting in manus tracks that are simple linear or ovoid shapes. Pes tracks occur both individually and clustered, and are represented by multiple parallel to subparallel lineations with length to width ratios between 0.7–1.4 depending on the species (Table 6).

DISCUSSION

Observed Terrestrial Behaviors of Bats

All bats observed in this study performed terrestrial behaviors previously described in the literature, although these behaviors are newly described in many of the taxa included here. In our study, *Desmodus rotundus* performed the diagonal sequence walk (defined by Hildebrand, 1985) in that a forelimb making contact with the sediment immediately followed the hindlimb on the opposite side of the body. Riskin et al. (2006), in contrast, observed *D. rotundus* to perform a lateral sequence walk, more typical of quadrupedal tetrapods. More work must be conducted in order to determine the conditions in which *Desmodus* uses each gait, and whether or not other desmodontines also display this variability in choice of walking gait. When moving rapidly, *Desmodus* performed the bound described by Riskin and Hermanson (2005) and Riskin et al. (2006)—an asymmetrical gait in which the forelimbs are used to initiate the aerial component of the gait rather than the hindlimbs as in other bounding tetrapods. This behavior has been described as an independently evolved run, and has only ever been observed in *D. rotundus* (Riskin and Hermanson, 2005; Riskin et al., 2006). The breaststrokeline crawl—described by Jones and Hasiotis (in review) from the phyllostomid bat *Carollia perspicillata*—was performed by *Carollia perspicillata*, *C. sowelli*, *Dermanura phaeotis*, *Hylonycteris underwoodi*,

Lonchorhina aurita, *Micronycteris microtis*, and *Saccopteryx bilineata*. The searching behavior—documented by Dietz (1973) and Jones and Hasiotis (in review) for species of phyllostomid and vespertilionid bats—was performed by *Artibeus lituratus*, *C. perspicillata*, *C. sowelli*, *D. phaeotis*, *L. aurita*, and *S. bilineata* (Table 7).

Within phyllostomids, terrestrial behaviors exhibited in this study align clearly to pelvic and hindlimb morphology defined by Vaughan (1970) and Schutt and Simmons (2006). *Desmodus rotundus* is the only Type 3 bat used in this study and is the only phyllostomid to perform such typical quadrupedal gaits as the diagonal sequence walk and the bound. All other phyllostomids we observed represent the Type 1 pelvic and hindlimb morphology, and all performed the breaststrokelike crawl and/or the nonambulatory searching behavior. No discernable differences between the terrestrial abilities of any of the nondesmodontine phyllostomid subfamilies were observed. No individuals of *Desmodus* performed behaviors observed in Type 1 bats, and no Type 1 phyllostomids performed behaviors representative of Type 3 bats. Previous studies have shown that some Type 1 phyllostomids are capable of at least the diagonal sequence walk, but these instances are rare in adults (Jones and Hasiotis, in review) or restricted to juveniles (Dietz, 1973).

Terrestrial behaviors of the Type 2 emballonurid *Saccopteryx bilineata* are indistinguishable from those of the Type 1 phyllostomids used in this study. *Saccopteryx* performed only the breaststrokelike crawl and searching behavior, and was not noticeably different in terrestrial competency from the Type 1 phyllostomids, which are the least competent. Despite differences in feeding and foraging habits between the insectivorous *Saccopteryx* and such varied phyllostomid taxa as the frugivorous *Carollia* and *Dermanura* and nectarivorous *Hylonycteris*, terrestrial competency was identical.

These observations are significant, as previous studies have demonstrated that Type 2 bats exhibit greater terrestrial competency than Type 1 bats. Lawrence (1969) reported varied, but nonetheless adept, terrestrial behavior in three species of the Type 2 family Vespertilionidae. Dietz (1973) mentioned proficient terrestrial locomotion in the vespertilionid *Antrozous pallidus*. *Antrozous* has been reported to forage for prey on the ground (Orr, 1954) unlike *Saccopteryx*, which feeds primarily on insects in flight (Bradbury and Vehrencamp, 1976). More research, therefore, must be conducted on Type 2 bats to determine their variability in terrestrial behavior, as well as any possible morphological or ecological basis for the differences in terrestrial competency seen in this group.

Track and trackway morphology recorded in casts

Tracks produced by bats in this study are recognizable in casts, with those produced by *Desmodus rotundus* featuring the most unique morphology compared to the Type 1 and 2 bats. *Desmodus* manus tracks, unlike those produced by the Type 1 and 2 bats, are often more complex than simple linear or ovoid shapes and include impressions of both the digit I and the wrist and distal forearm. *Desmodus* is also the only bat to regularly produce consistent trackways that are recognizable by manus tracks more distal to the trackway midline than the pes tracks and, in the case of the bounding behavior, paired manus and pes impressions. In these trackways, in addition to a midline, there is evidence of the directionality or position of the bat, including the orientation of digit I relative to the rest of the manus impression and the position of pes tracks relative to the manus.

Nondesmodontine phyllostomids and *Saccopteryx* tracks are nearly indistinguishable from each other based on the plasters casts. Manus tracks are simple linear or ovoid shapes,

ranging from ~2–4 times as long as they are wide, and are not obviously associated with any trackway. Pes tracks are less frequent than manus tracks in these bats, but are similarly not associated with trackways. Pes tracks may be isolated, or occur as part of clusters of pes tracks that correspond to the searching behavior. Arcuate traces were observed in most nondesmodontine taxa, including those that performed the breaststrokeline crawl but not the searching behavior and those that performed the searching behavior but not the breaststrokeline crawl (Table 7). Arcuate traces likely correspond most often to the breaststrokeline crawl, but can also be produced by digit I when extending or retracting the wings or rotating during the searching behavior. This behavior with wings extended was observed in *Saccopteryx*, *Micronycteris*, and *Lonchorhina*. This is the first observation of arcuate lineations produced during the searching behavior.

Bat traces produced in this study also resemble several morphotypes of invertebrate trace fossils. *Planolites* (Fig. 15A), which is an unbranched, horizontal simple burrow (e.g., Pemberton and Frey, 1982), could be confused with arcuate traces or manus tracks due to their simple morphologies (see Fig. 13). *Palaeophycus* (Fig. 15B) is similar to *Planolites*, but is a lined burrow (e.g., Pemberton and Frey, 1982). Arcuate traces or manus tracks can be distinguished from these morphotypes by their repetition in curvature and occurrence in conjunction with morphologies identical to pes tracks and other manus tracks. *Sagittichnus* (Fig. 15C), which are small (< 3 mm long), slightly linear or arrow-shaped impressions (e.g., Garvey and Hasiotis, 2008), may appear similar to clustered pes tracks and closely aligned manus tracks. These bat traces can be distinguished from *Sagittichnus* by their similar orientations and close proximity of more linear impressions (pes tracks), and random occurrence, variable dimensions, and orientation of manus tracks (see Figs. 8, 11–14). Many longer, discontinuous manus tracks

(see Fig. 13) may be confused with *Treptichnus* (Fig. 15D, E), subhorizontal, straight to curved, zigzagged burrow segments with vertically oblique tubes that form nodes in truncated trails (e.g., Miller, 1889; Seilacher, 1955). Such manus tracks can be delineated from *Treptichnus* by the lack of curvature and nodes of each segment that results in zigzag pattern. Bilobate manus impressions (see Fig. 14) resemble the resting trace *Rusophycus* (Fig. 15F), which are bilobate impressions that taper to one end with oblique to transverse striations in each lobe (e.g., Miller, 1889; Garvey and Hasiotis, 2008). Such manus tracks can be differentiated from *Rusophycus* by the lack of internal striations and definitive taper. Overall, the best way to distinguish bat tracks and trackways from invertebrate trace fossils is by the association, repetition, and morphologies of tracks and traces characteristic of tetrapod and bat locomotion (e.g., Lawrence, 1969; Hildebrand, 1989; Jones and Hasiotis, in review; and data herein). Also, bat traces will lack intricate morphologies (e.g., branching, lining, geometric patterns) and detailed, internal striations within individual traces that are typical of invertebrate trace fossils (e.g., Bromley, 1996; Hasiotis, 2004, 2008).

Implications for the identification of bat tracks in the fossil record

The bat body fossil record is poor (Eiting and Gunnell, 2009); however, recognition of the track and trackway morphologies produced by bats can help to determine their dispersal patterns and paleobiogeography, and elucidate the evolutionary history. Trace fossils have been used to infer the presence of organisms in the fossil record in the absence, either temporally or geographically, of body fossils (e.g., Hasiotis, 2003, 2004, 2008; Lockley et al., 2007; Niedźwiedzki et al., 2010; Narkiewicz and Narkiewicz, 2015). The characterization of track morphology and variability produced by bats could be used to extend the known occurrences of

bats in Eocene and older deposits. Our description of phyllostomid and emballonurid tracks can serve as a reference for possible bat tracks in the Cenozoic rock record, especially in determining tracks produced by bats of these families. For example, the Phyllostomidae possess a ghost lineage of over 20 million years, with little fossil evidence of the radiation that produced the diversity typical of the family. The fossil record of the Phyllostomidae dates to the middle Miocene La Venta fauna of Colombia, between 13.8–11 Ma (Savage, 1951; Czaplewski, 1997). Phyllostomid taxa known from this unit include *Notonycteris magdalensis* (a large predatory phyllostomine similar to modern *Vampyrum* or *Chrotopterus*), a species of the smaller phyllostomine *Tonatia*, an indeterminate species of phyllostomine, and the glossophagine *Palynephyllum antimaster* (Czaplewski, 1997; Czaplewski et al., 2003). Additional fossil phyllostomids are known from the Pleistocene and Holocene of North and South America and the Caribbean, including members of the subfamilies Desmodontinae, Phyllostominae, and Stenodermatinae (e.g., Anthony 1917a, b; Woloszyn and Silva Taboada, 1977; Morgan et al., 1988; Morgan, 1991). Molecular studies place the origin of Phyllostomidae between 42–34 Ma, with the radiation that produced the current subfamilies and their unique ecological niches occurring between 30–19 Ma (Datzmann et al., 2010; Baker et al., 2012). Thus, tracks and trackways attributable to the Phyllostomidae could fill in the 20+ million-year gap in the fossil record.

The fossil record of the Emballonuridae is much more extensive than that of the Phyllostomidae, with specimens known from both the eastern and western hemispheres. The earliest emballonurid body fossils date to the Eocene, and include the remarkably well-preserved *Tachypteron franzeni* from the Grube Messel oil shale in Germany (Storch et al., 2002). Most Eocene taxa currently known are from Europe, with other genera found in France and the United

Kingdom (e.g., Crochet et al., 1981; Marandat et al., 1993; Hooker, 1996). By the latest Eocene, emballonurids are known from northern Africa (Gunnell et al., 2008), and by the Oligocene, they are present in North America and the Middle East (Sigé et al., 1994; Morgan and Czaplewski, 2003). By the Miocene, emballonurids had spread to Sub-Saharan Africa, South America, and Southeast Asia (Butler and Hopwood, 1957; Mein and Ginsburg, 1997; Czaplewski et al., 2003). Identification of emballonurid tracks will help clarify dispersal patterns in this group. By understanding how a particular family of bats was able to spread across the globe long after the breakup of Pangea (e.g., Stanley and Luczaj, 2015), we can begin to understand the advantages and limitations to dispersal in these flying mammals.

CONCLUSIONS

This is the first study to address the terrestrial ability and trackmaking behaviors of a wide variety of phyllostomid species belonging to most of the major subfamilies, and the first to address the terrestrial ability of any member of the cosmopolitan family Emballonuridae. Bats used in this study demonstrated a clear division in terrestrial ability, with the Type 3 taxon *Desmodus rotundus* performing previously recognized quadrupedal gaits, whereas Type 1 and 2 taxa belonging to the Phyllostomidae and Emballonuridae only performed the breaststroke-like crawl and the searching behavior. Some Type 1 and Type 2 species may be capable of performing such gaits as the diagonal and lateral sequence walks based on reviews of previous literature (e.g., Lawrence, 1969; Dietz, 1973; Jones and Hasiotis, in review), however, these gaits are likely not employed in the case of nondesmodontine phyllostomids.

Our results only partially support the Type 1–3 pelvic and hindlimb morphologic distinctions as an indicator of terrestrial ability in bats. Type 1 taxa in this study are all poor

walkers, whereas the Type 3 *Desmodus* is very terrestrially adept. The Type 2 *Saccopteryx bilineata* is as poorly suited to terrestrial locomotion as the Type 1 taxa, despite earlier published reports of Type 2 species performing coordinated terrestrial gaits (Lawrence, 1969; Dietz, 1973). This is noteworthy, as the Type 2 classification appears to include several different levels of terrestrial competency. Further study is needed to determine if the difference in Type 2 terrestrial ability is due to ecology or to subtle variations in pelvic and hindlimb anatomy.

Tracks produced by bats in this study are recognizable in casts, and include (1) manus tracks that range from simple, linear shapes to robust L-shaped impressions produced by both digit I and the wrist and distal forearm; (2) pes tracks comprised of multiple parallel or subparallel lineations and may occur as isolated tracks or as part of a cluster of pes tracks corresponding to searching behavior; and (3) arcuate lineations produced by the manus and corresponding to searching behavior and/or breaststrokelike crawl. Trackways with a discernable midline were only produced by *Desmodus*, and feature manus tracks that are more prominent and more distal to the midline of the trackway than the pes tracks.

Results of this research fill the gaps in our understanding of the terrestrial abilities within Chiroptera and help to establish a template for what bat tracks and trackways would look like in the fossil record. The long Cenozoic body fossil record of bats and the variety of niches, body plans, and terrestrial competency adopted by extant taxa indicate that identification of bat trace fossils in the sedimentary rock record may be possible in time-equivalent strata in which body fossils are known, as well as in older and younger strata. Bat trace fossils may be confused with such invertebrate trace fossils as *Planolites*, *Rusophycus*, *Sagittichnus*, and *Treptichnus*, but can be distinguished from them based on morphologic criteria and pattern recognition. Overall, these

data, in turn, can be used to fill in gaps in the bat body fossil record, and help to elucidate patterns of evolution and global dispersal of bats.

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FIGURE CAPTIONS

Figure 1—Experimental setup with *Desmodus rotundus*.

Figure 2—Video screen captures of *Desmodus rotundus* bounding behavior. A) Bat positions both wrists anterior to tip of snout with pedes proximal to body. B–C) Body propelled forward as wrists and digit I remain planted, resulting in position with wrists posterior to shoulders and pedes distal to body. D) Pedes picked up and brought proximal to body at same time as forelimbs lifted and moved forward. E) Bat returns to initial position with wrists anterior to tip of snout. F) Motion repeated.

Figure 3—Video screen captures of *Desmodus rotundus* diagonal sequence walk. A) Initial position with left manus posterior to head. B–C) Left manus picked up and moved to position with wrist roughly even with eyes, body moved forward so right wrist now even with shoulders. D) Right manus picked up and moved into position with wrist even with eyes. E) Left pes picked up and brought proximal to body. F) Right pes picked up and brought proximal to body, in this case before left pes planted. G–H) Right pes planted and bat returns to original position.

Figure 4—Video screen captures of *Hylonycteris underwoodi* breaststrokeliike crawl. A) Initial position with both wrists roughly even with eyes. B–C) While keeping wrists planted bat propels body forward resulting in position with wrists roughly even with shoulders. D–E) As bat lands it swings arms forward. F–H) Bat returns to initial position with wrists even with eyes.

Figure 5—Video screen captures of *Saccopteryx bilineata* searching behavior. A) Initial position with feet stationary and distal to body. B–C) Bat retracts right pes then extends it distal to body. D–F) Bat plants right pes and retracts then extends left pes. G–H) Left pes planted and bat begins to retract right pes as it leans to right.

Figure 6—*Desmodus rotundus* bounding trackway cast showing outlines of manus and pes tracks. Scale bar 5 cm.

Figure 7—*Desmodus rotundus* track morphologies. A) Manus track with thin and elongate digit I and robust wrist impressions. B) Pes track. Scale bars 1 cm.

Figure 8—*Micronycteris microtis* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bar 5 cm.

Figure 9—*Hylonycteris underwoodi* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 10—*Dermanura phaeotis* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 11—*Artibeus lituratus* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 12—*Lonchorhina aurita* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 13—*Carollia sowelli* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 14—*Saccopteryx bilineata* cast showing outlines of manus and pes tracks lacking any discernable trackways. Scale bars 5 cm.

Figure 15—Invertebrate trace fossils similar to traces produced by bats in this study. A) *Planolites* (upper terminating at a *Rusophycus*). B) *Palaeophycus* (both lined and unlined). C) Clusters of *Sagittichnus*. D–E) *Treptichnus*. F) *Rusophycus*. Photos A, C, D, and F courtesy of S.R. Hammersburg, photo B courtesy of A.M. Jackson, photo E courtesy of J.D. Hogue. Scale bars 1 cm.

TABLE CAPTIONS

Table 1—Morphological characteristics of Type 1, 2, and 3 bats as defined by Vaughan (1970) and Schutt and Simmons (2006).

Table 2—Bat individuals and species observed in locomotion and trackmaking trials during this study.

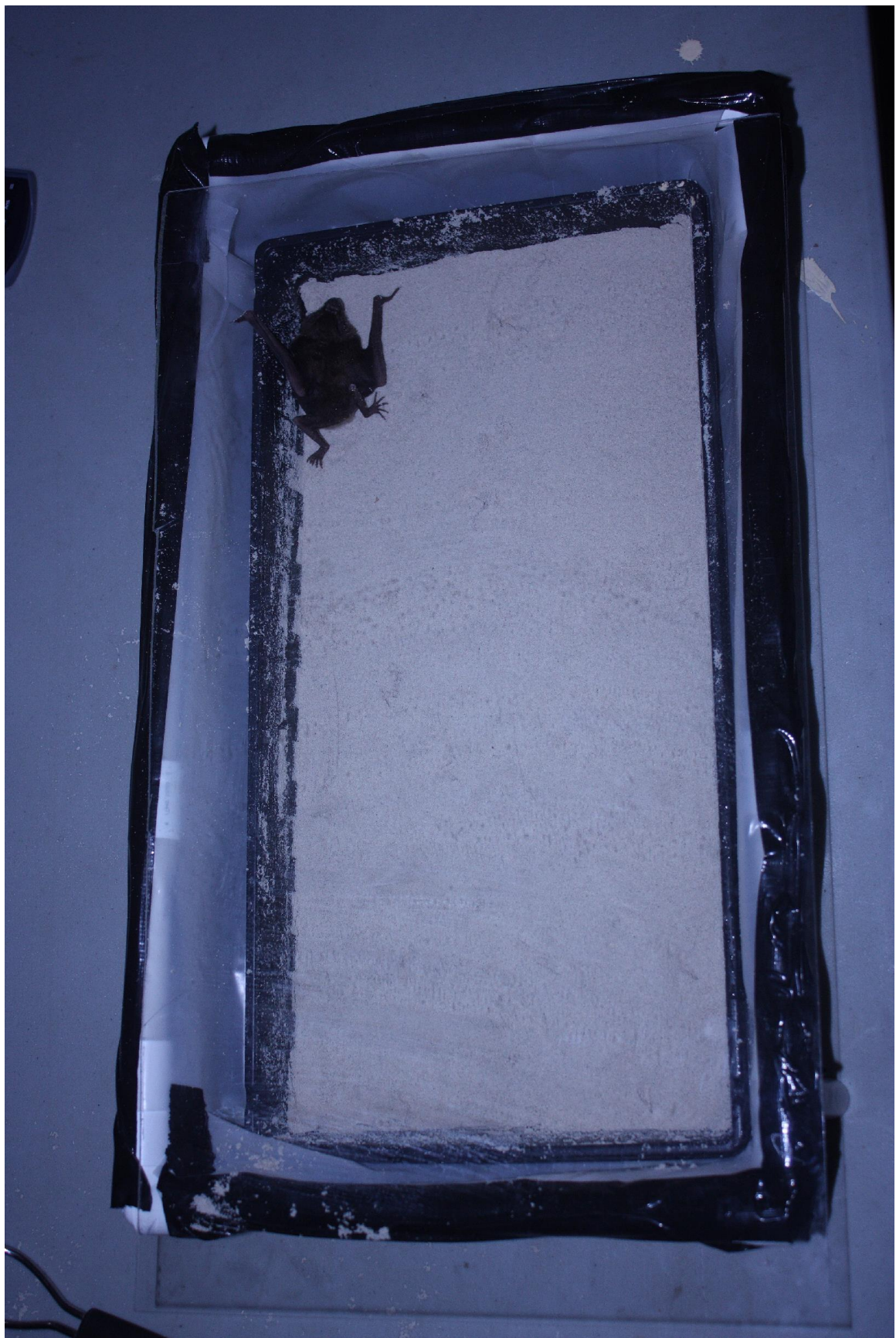
Table 3—Trackway sample weights and percent moisture of sand.

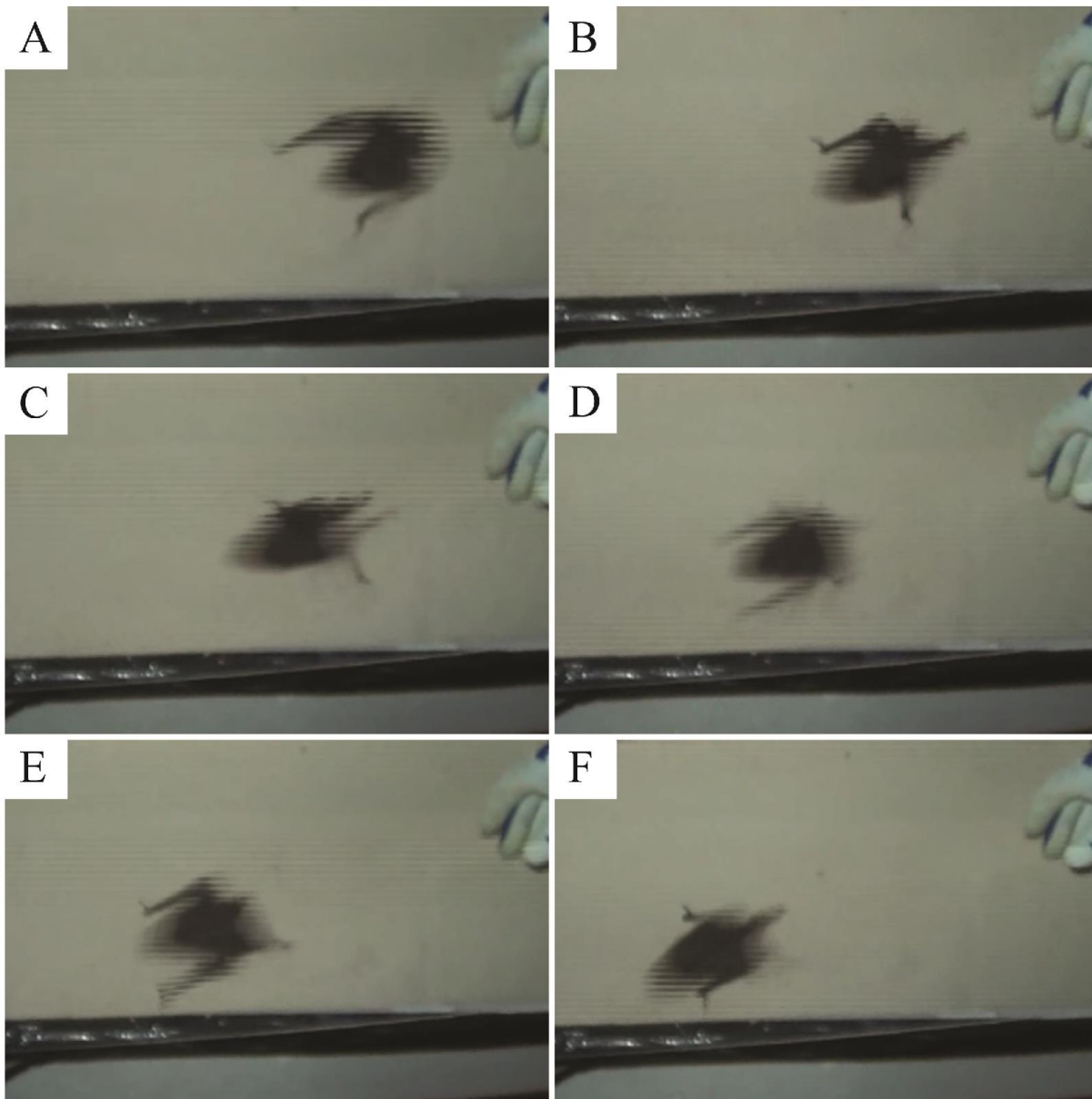
Table 4—Terrestrial behaviors observed in previous studies.

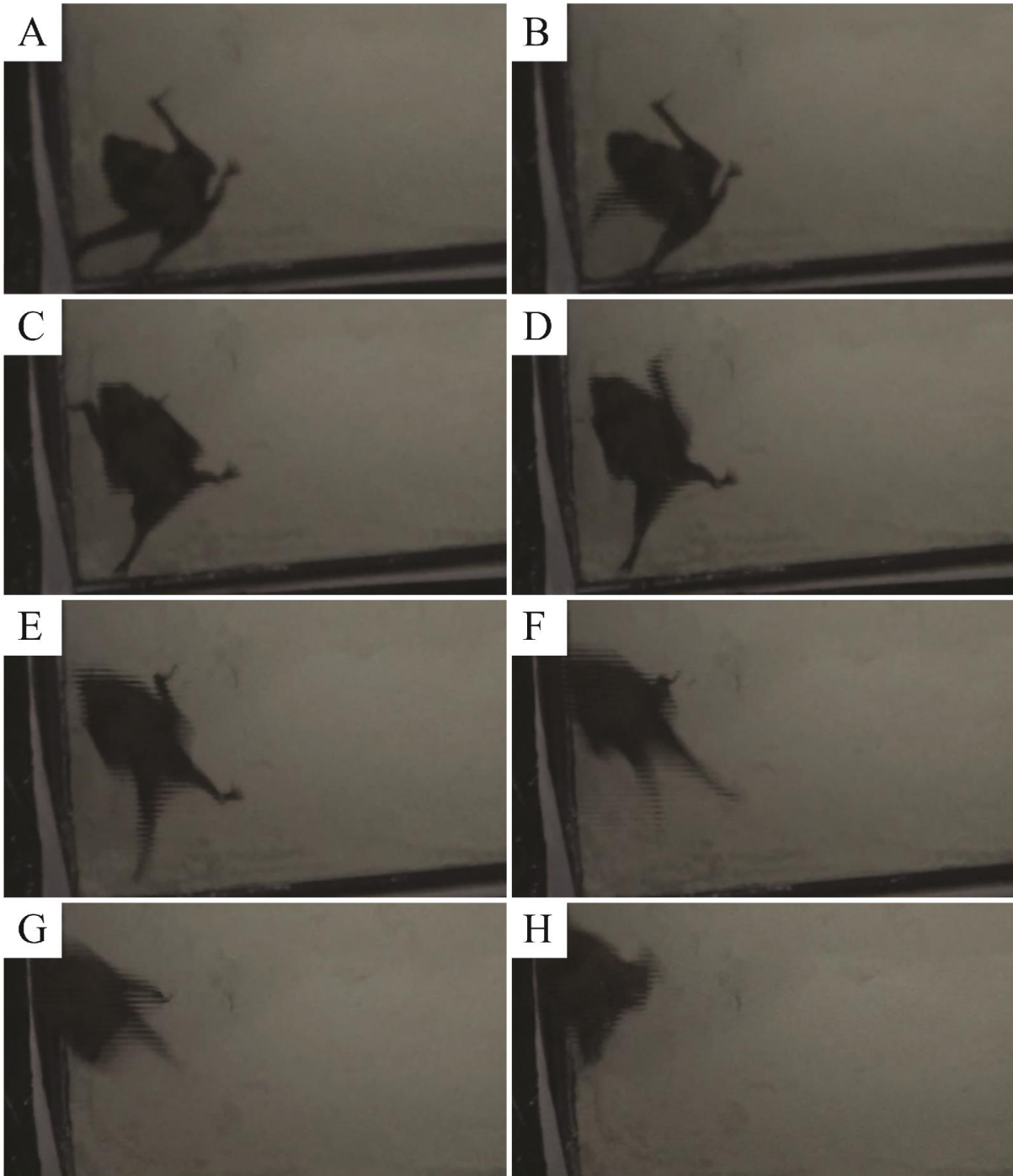
Table 5—Average track measurement by species.

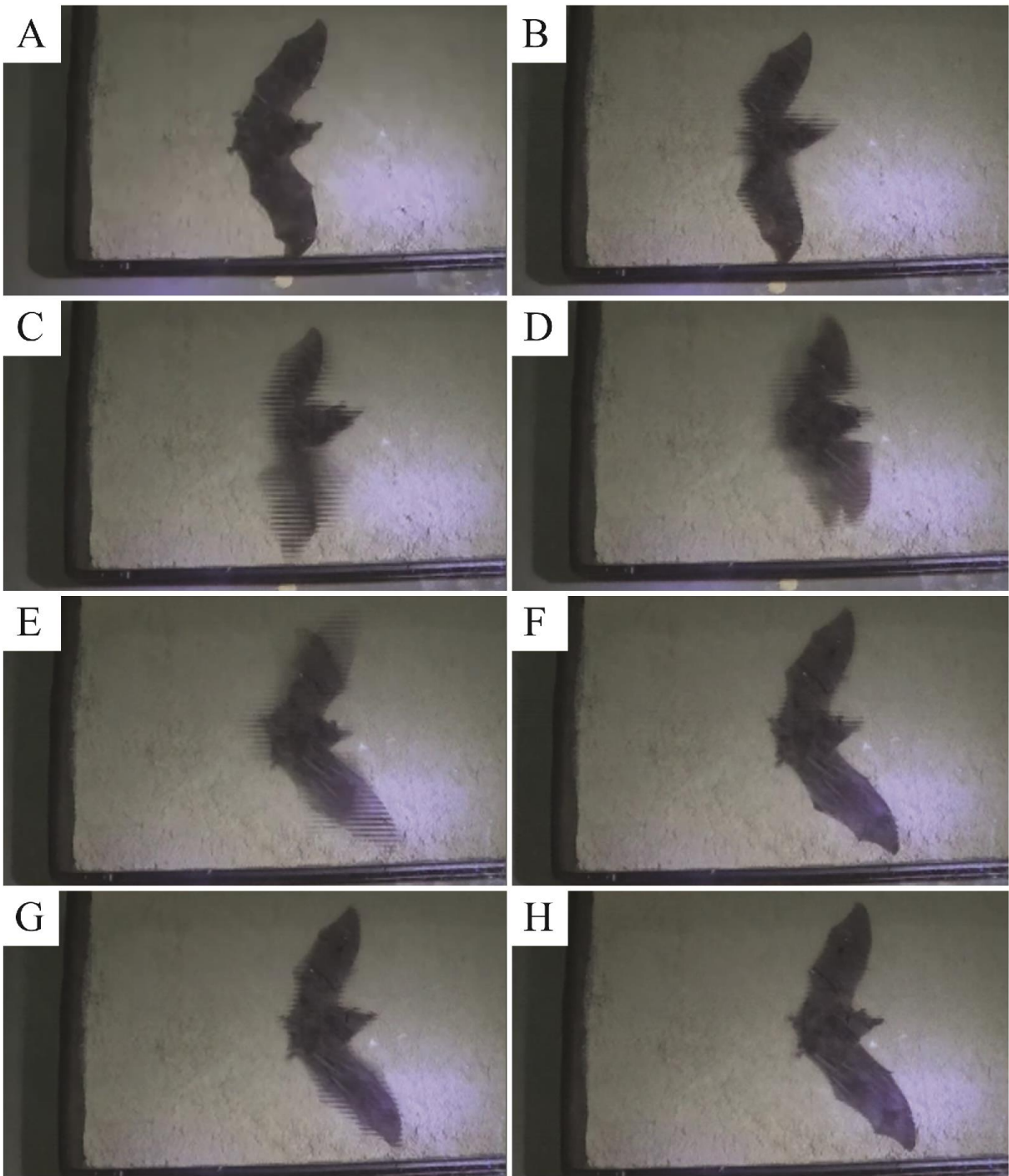
Table 6—Length to width ratios of manus and pes tracks by species.

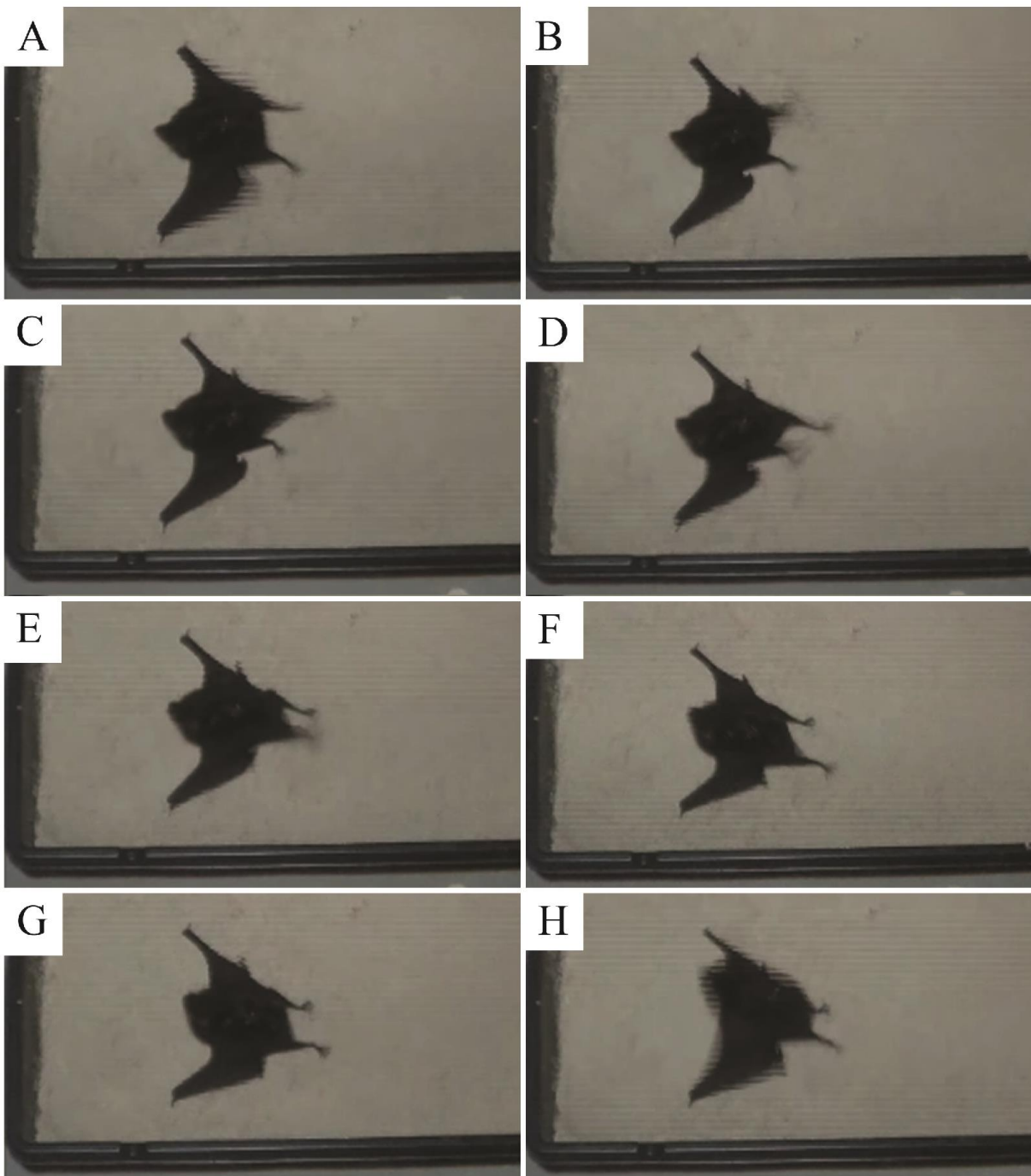
Table 7—Behaviors observed and track morphology produced by bat species included in this study.

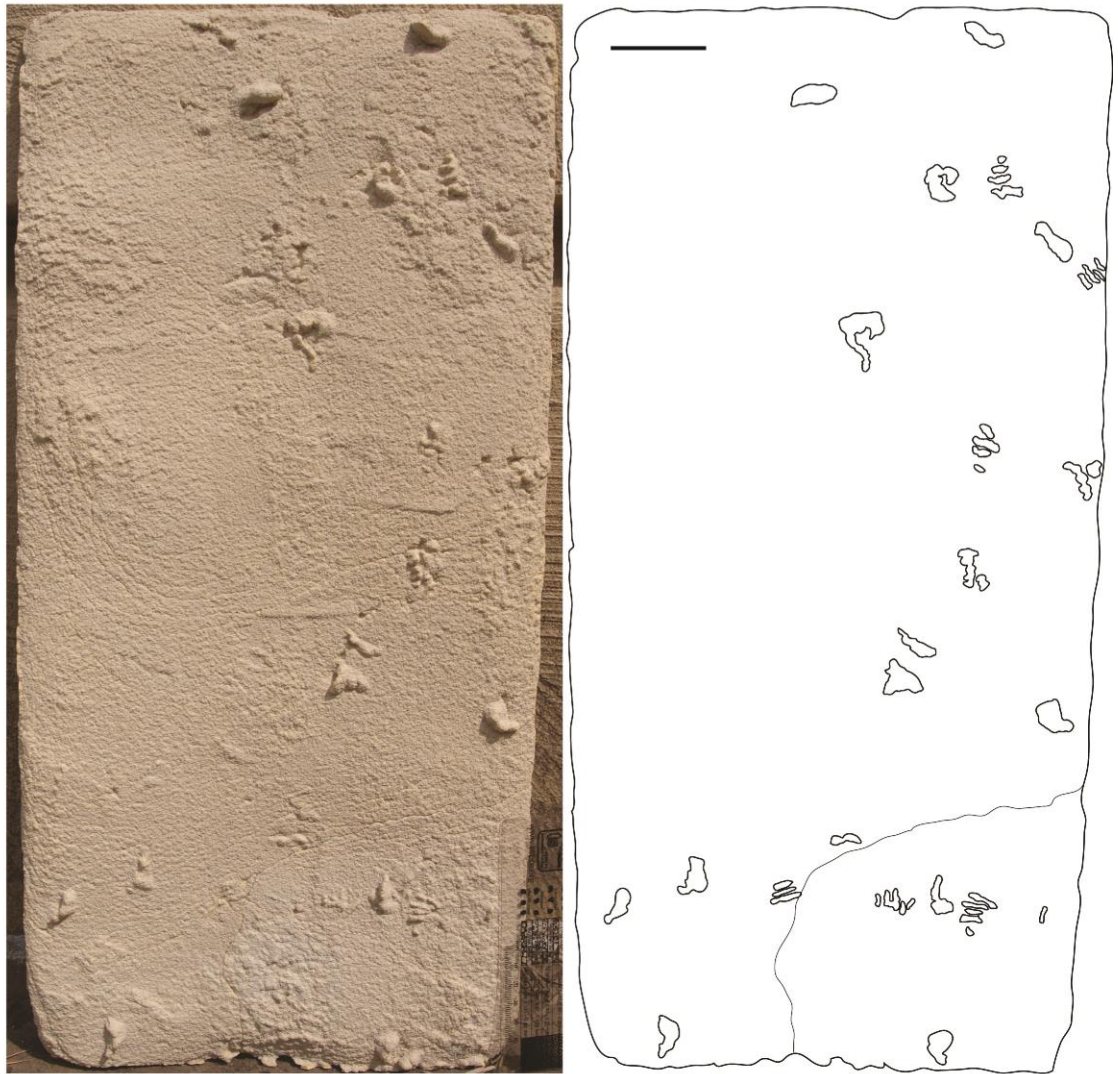


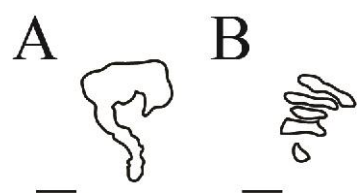


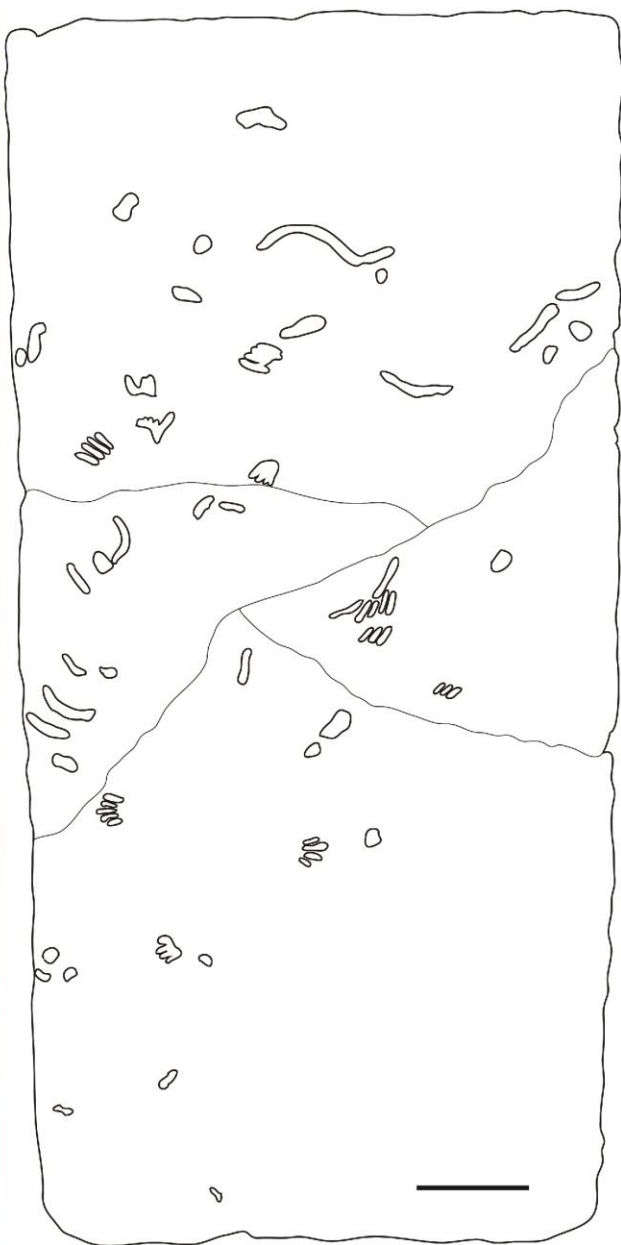
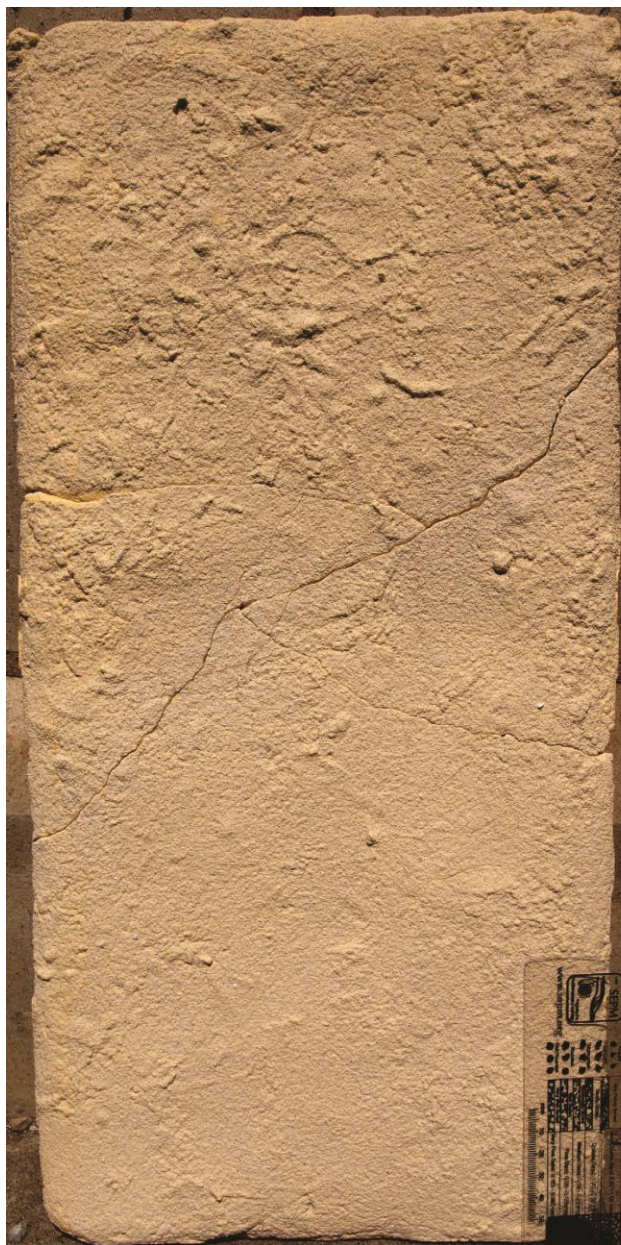


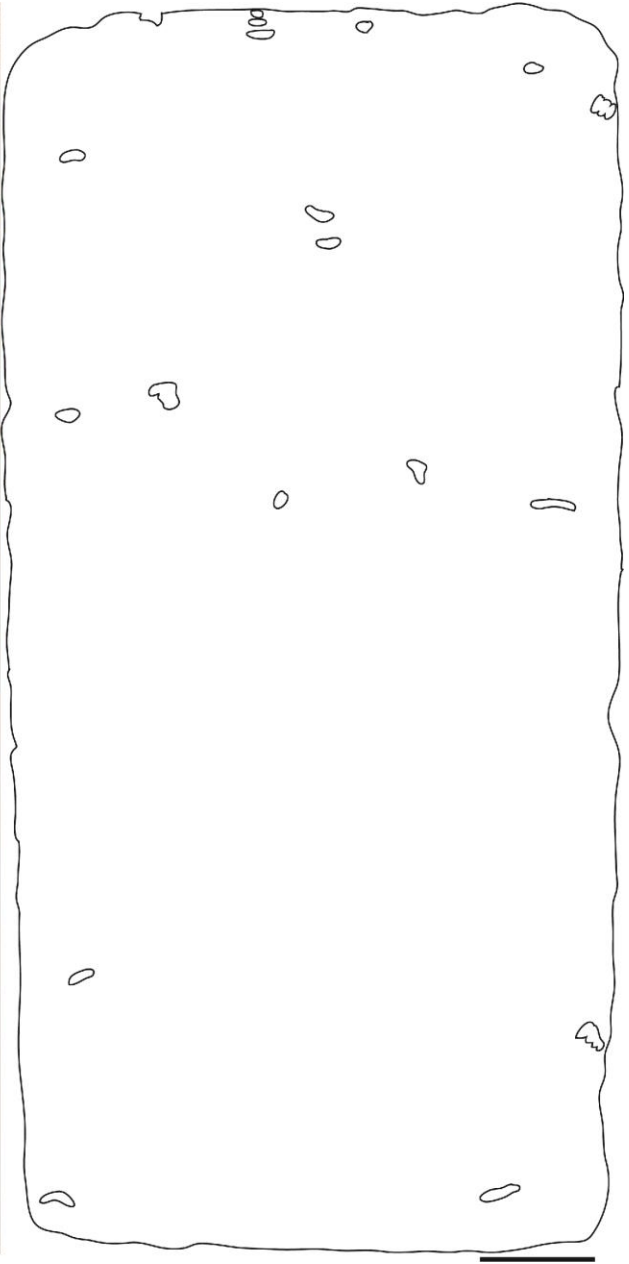


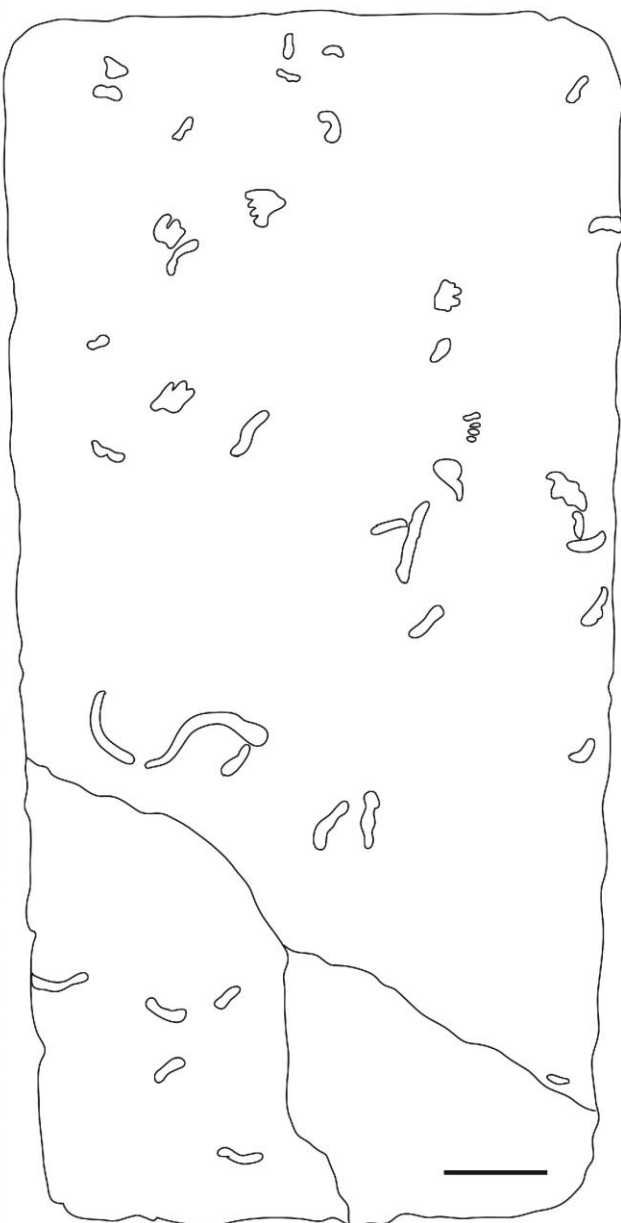
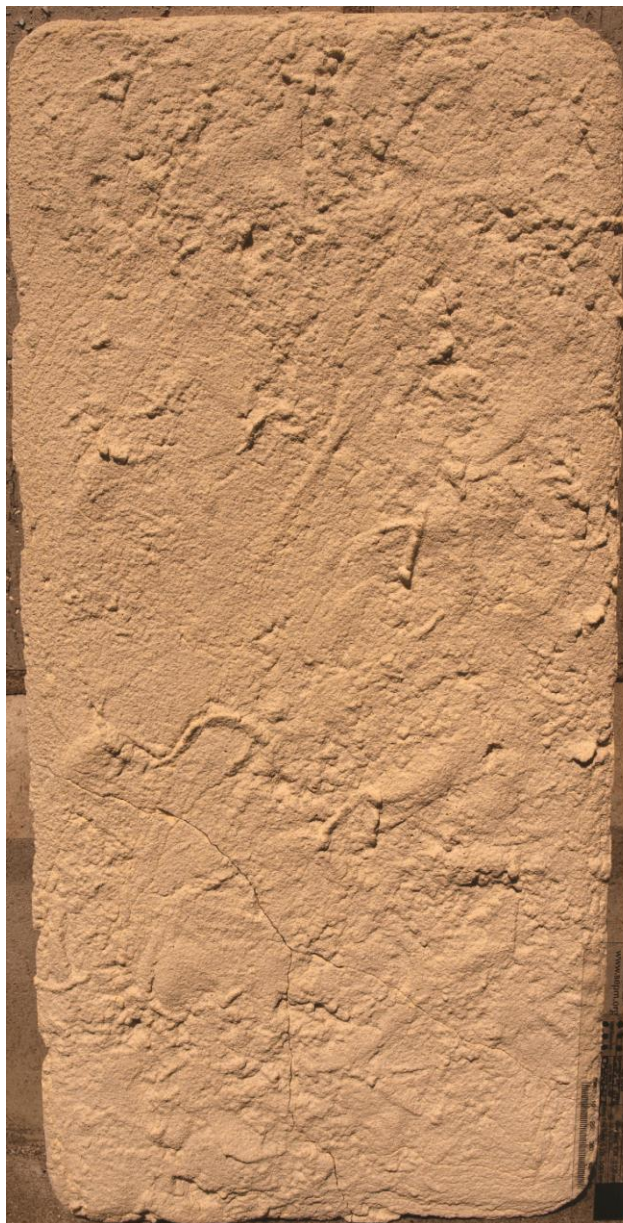




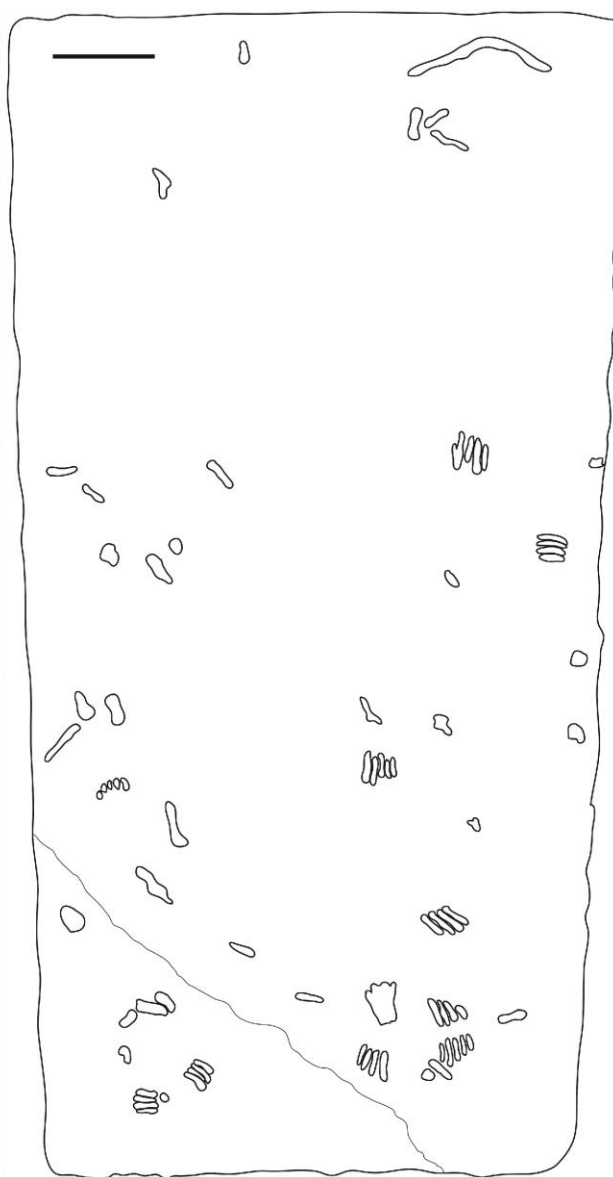
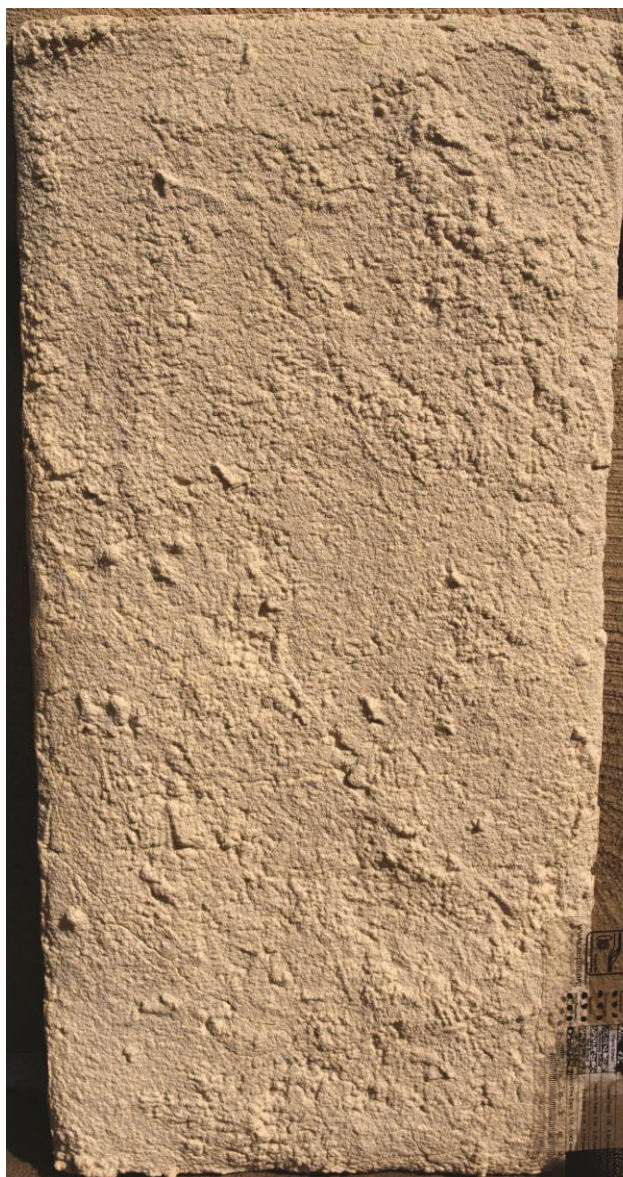


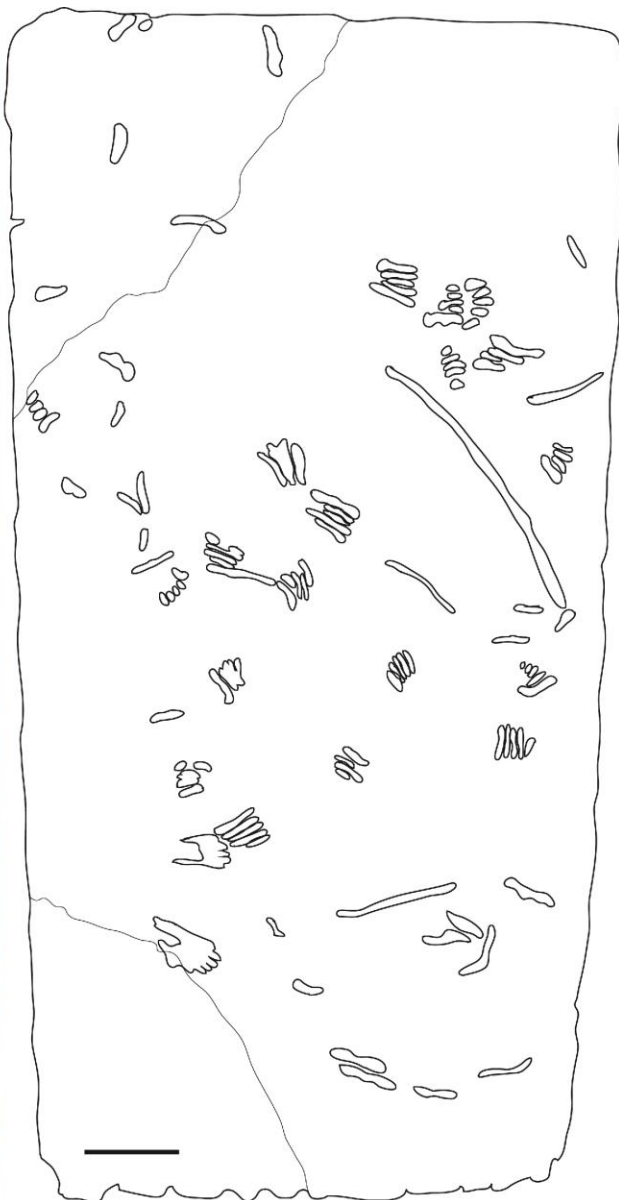


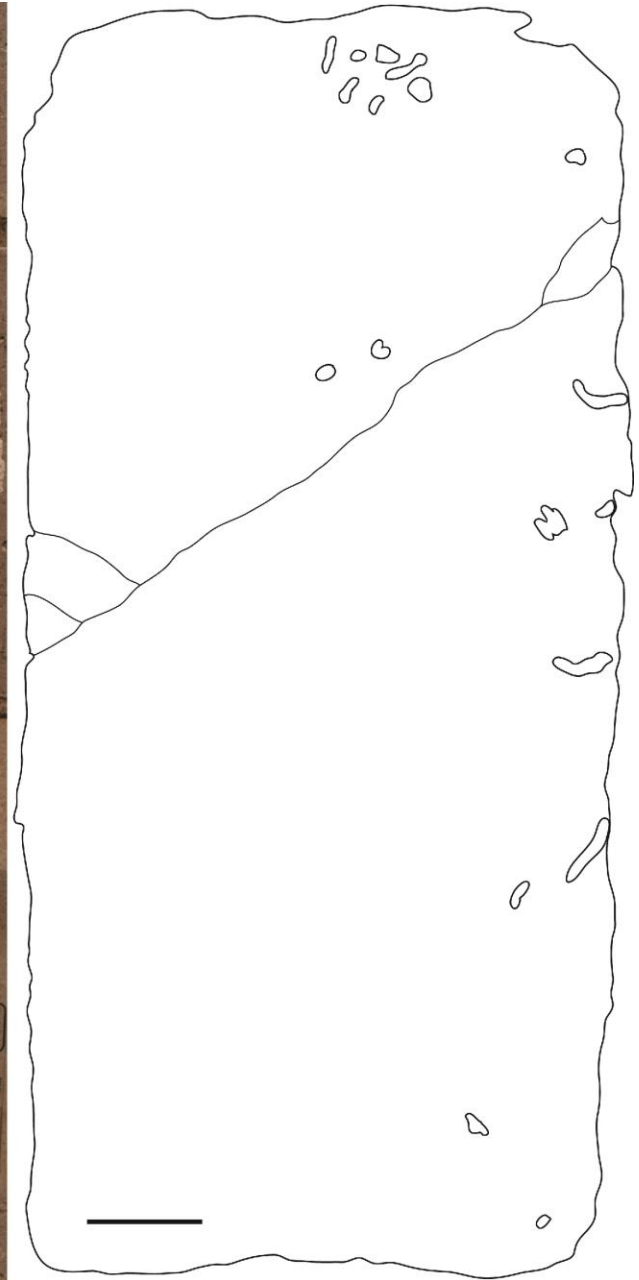
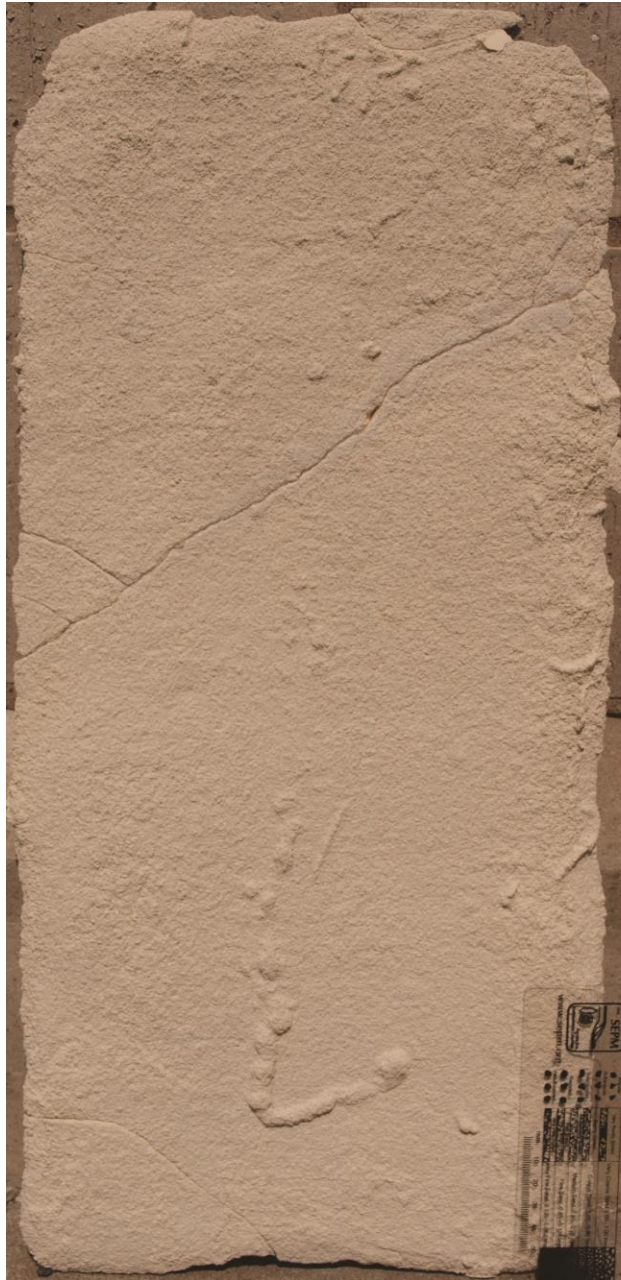


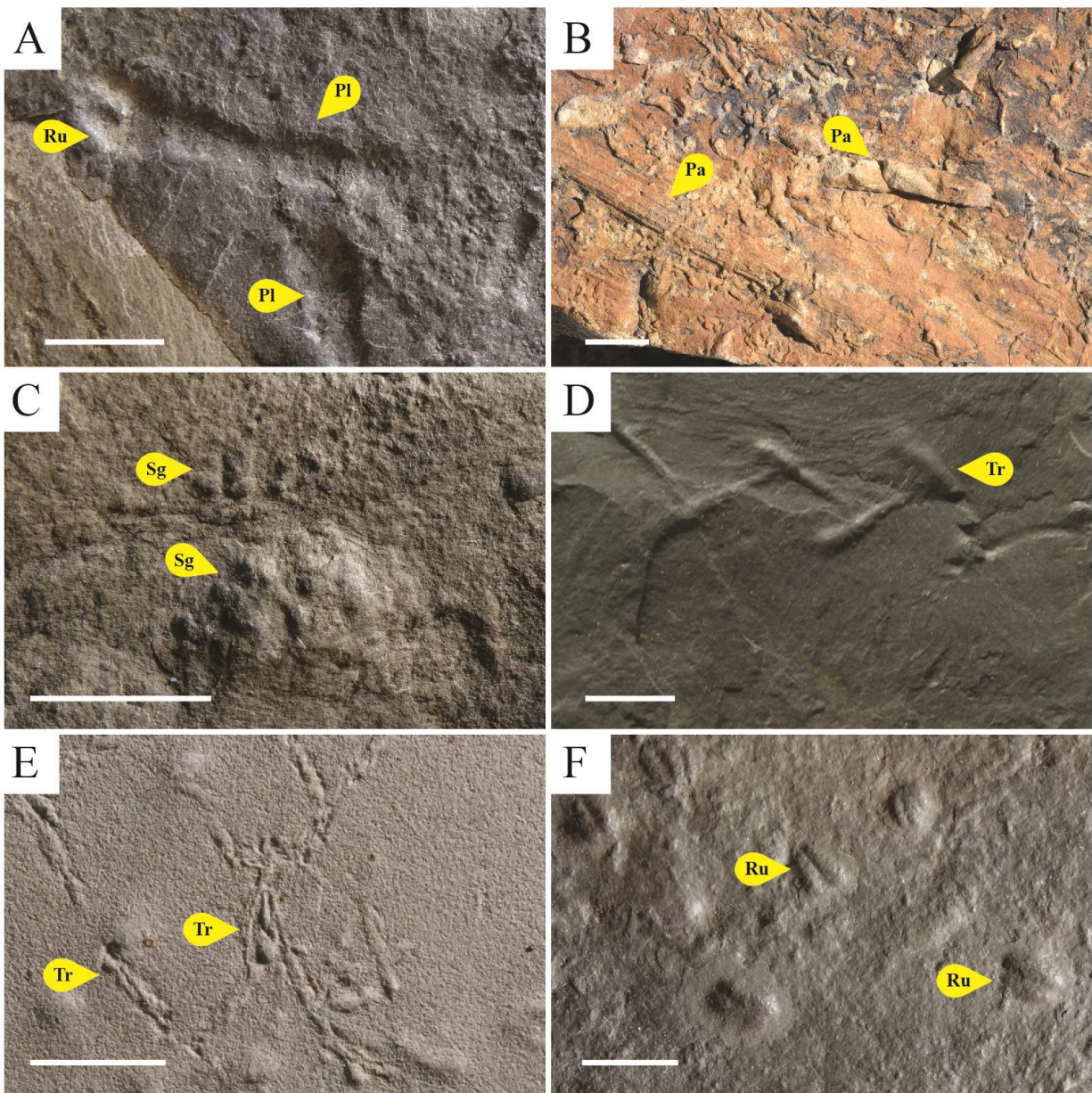












Morphotype	Taxa	Femur orientation	Fibula	Pelvis	Acetabulum	Presumed terrestrial competency
Type 1	Phyllostomidae	caudal, slightly dorsal	incomplete	laterally compressed, gracile	small	poor
Type 2	Emballonuridae, Nycteridae, Natalidae, Vespertilionidae, some Phyllostomidae (e.g., <i>Vampyrum</i>)	lateral	incomplete	intermediate to Types 1 & 3	intermediate	good
Type 3	Desmodontinae (Phyllostomidae), Molossidae, <i>Mystacina</i>	anterolateral	complete in most species	broad, robust	large	very good

Species	Weight (g)	Forearm length (mm)	Maturity	Family, subfamily	Feeding habit/niche	Pelvic and hindlimb morphology
<i>Saccopteryx bilineata</i>	11.8	46.8	Adult	Emballonuridae	Insectivore	Type 2
<i>Saccopteryx bilineata</i>	7	43.3	Adult	Emballonuridae	Insectivore	Type 2
<i>Carollia perspicillata</i>	22.2	44	Adult	Phyllostomidae, Carollinae	Generalist frugivore	Type 1
<i>Carollia sowelli</i>	19	39	Adult	Phyllostomidae, Carollinae	Generalist frugivore	Type 1
<i>Desmodus rotundus</i>	43.8	63.8	Juvenile	Phyllostomidae, Desmodontinae	Sanguinivore	Type 3
<i>Desmodus rotundus</i>	49	60.4	Adult	Phyllostomidae, Desmodontinae	Sanguinivore	Type 3
<i>Desmodus rotundus</i>	38.3	64.8	Adult	Phyllostomidae, Desmodontinae	Sanguinivore	Type 3
<i>Desmodus rotundus</i>	33.6	59.1	Adult	Phyllostomidae, Desmodontinae	Sanguinivore	Type 3
<i>Hylonycteris underwoodi</i>	7.1	33.3	Adult	Phyllostomidae, Glossophaginae	Nectarivore	Type 1
<i>Lonchorhina aurita</i>	14.6	51.8	Juvenile	Phyllostomidae, Phyllostominae	Insectivore	Type 1
<i>Micronycteris microtis</i>	6.2	33.7	Juvenile	Phyllostomidae, Phyllostominae	Insectivore	Type 1
<i>Artibeus lituratus</i>	>75	74.2	Adult	Phyllostomidae, Stenodermatinae	Frugivore	Type 1
<i>Dermanura phaeotis</i>	14.8	40.4	Adult	Phyllostomidae, Stenodermatinae	Frugivore	Type 1

Species	Pre-dry weight (g)	Dry weight (g)	Percent moisture
<i>Saccopteryx bilineata</i>	3.13	2.81	0.10
<i>Saccopteryx bilineata</i>	7.97	7.37	0.08
<i>Carollia perspicillata</i>	4.51	4.49	0.00
<i>Carollia sowelli</i>	1.61	1.44	0.11
<i>Desmodus rotundus</i>	4.69	4.42	0.06
<i>Desmodus rotundus</i>	4.19	3.95	0.06
<i>Desmodus rotundus</i>	3.02	2.76	0.09
<i>Desmodus rotundus</i>	4.5	4.01	0.11
<i>Hylonycteris underwoodi</i>	4.69	4.3	0.08
<i>Lonchorhina aurita</i>	4.8	4.57	0.05
<i>Micronycteris microtis</i>	5.21	4.9	0.06
<i>Artibeus lituratus</i>	2.44	2.17	0.11
<i>Dermanura phaeotis</i>	4.04	3.86	0.04

Species	Family	Subfamily	Terrestrial behaviors	Figures	Reference(s)
<i>Molossus</i> sp.	Molossidae		variable stride walk	No	Dietz, 1973
<i>Tadarida</i> sp.	Molossidae		"close strides and gaits"	No	Dietz, 1973
<i>Pteronotus parnellii</i>	Mormoopidae		variable, sprawling crawl	Photographs	Riskin et al., 2005
<i>Mystacina tuberculata</i>	Mystacinidae		lateral sequence walk	Photographs	Riskin et al., 2006; Schutt and Simmons, 2006
<i>Natalus tumidirostris</i>	Natalidae		None	No	Riskin et al., 2005
<i>Carollia perspicillata</i>	Phyllostomidae	Carollinae	searching; diagonal sequence walk; breaststroke-like crawl	Photographs	Jones and Hasiotis (in review)
<i>Desmodus rotundus</i>	Phyllostomidae	Desmodontinae	lateral sequence walk; bound	Photographs	Altenbach, 1979; Schutt et al., 1997; Riskin and Hermanson, 2005; Riskin et al., 2005; Riskin et al., 2006; Schutt and Simmons, 2006
<i>Diaemus youngi</i>	Phyllostomidae	Desmodontinae	lateral sequence gait; "hopping gait"	Photographs	Schutt et al., 1999; Riskin et al., 2005
<i>Leptonycteris</i> sp.	Phyllostomidae	Glossophaginae	searching; variable stride walk (juveniles only)	No	Dietz, 1973
<i>Macrotus</i> sp.	Phyllostomidae	Phyllostominae	searching; crawling (juveniles only)	No	Dietz, 1973
<i>Artibeus</i> sp.	Phyllostomidae	Stenodermatinae	sideways motion	No	Dietz, 1973
<i>Antrozous</i> sp.	Vespertilionidae		searching; variable stride walk; constant stride walk	No	Dietz, 1973
<i>Eptesicus</i> sp.	Vespertilionidae		searching; variable stride walk; constant stride walk	No	Dietz, 1973
<i>Eptesicus serotinus</i>	Vespertilionidae		lateral sequence walk	Stylized illustrations	Lawrence, 1969
<i>Myotis velifer</i>	Vespertilionidae		searching; variable stride walk; constant stride walk	No	Dietz, 1973
<i>Myotis yumanensis</i>	Vespertilionidae		variable stride walk; constant stride walk	No	Dietz, 1973
<i>Nyctalus noctula</i>	Vespertilionidae		normal and restricted run; leap-frogging	Stylized illustrations	Lawrence, 1969
<i>Parastrellus</i> sp.	Vespertilionidae		variable stride walk (fast)	No	Dietz, 1973
<i>Pipistrellus pipistrellus</i>	Vespertilionidae		lateral sequence walk; normal and restricted run	Stylized illustrations	Lawrence, 1969

	Manus tracks			Pes tracks		Arcuate tracks		
	Mean length (mm)	Mean width (mm)	Mean length (mm)	Mean width (mm)	Mean length (Straight line in mm)	Mean length along axis (mm)	Mean width (mm)	
<i>Saccopteryx bilineata</i>	8.6	3.8	18.1	13.3	32.5	35.9	3.5	
<i>Carollia perspicillata</i>	NA	NA	NA	NA	NA	NA	NA	
<i>Carollia sowelli</i>	15.3	3.9	16.4	15.0	57.9	59.4	2.7	
<i>Desmodus rotundus</i>	17.7	7.7	11.4	17.1	NA	NA	NA	
<i>Hylonycteris underwoodi</i>	9.7	2.9	9.6	13.8	NA	NA	NA	
<i>Lonchorhina aurita</i>	11.5	4.6	16.8	13.7	53.6	60.6	3.1	
<i>Micronycteris microtis</i>	10.6	4.7	10.5	11.6	32.5	31.4	4.7	
<i>Artibeus lituratus</i>	14.8	4.9	14.8	17.2	38.3	41.2	3.3	
<i>Dermanura phaeotis</i>	15.4	3.7	11.7	15.8	36.4	49.7	4.1	

	Manus (L:W)	Pes (L:W)
<i>Saccopteryx bilineata</i>	2.3	1.4
<i>Carollia perspicillata</i>	NA	NA
<i>Carollia sowelli</i>	3.9	1.1
<i>Desmodus rotundus</i>	2.3	0.7
<i>Hylonycteris</i> <i>underwoodi</i>	3.4	0.7
<i>Lonchorhina aurita</i>	2.5	1.2
<i>Micronycteris microtis</i>	2.3	0.9
<i>Artibeus lituratus</i>	3.0	0.9
<i>Dermanura phaeotis</i>	4.1	0.7

	Terrestrial behaviors observed				Traces produced			
	breaststroke-like crawl	searching	diagonal sequence walk	bound	arcuate	manus	pes	trackway
<i>Artibeus lituratus</i>		x			x	simple	isolated	No
<i>Carollia perspicillata</i>	x	x				NA	NA	NA
<i>Carollia sowelli</i>	x	x			x	simple	isolated and clustered	No
<i>Dermanura phaeotis</i>	x	x			x	simple	isolated	No
<i>Desmodus rotundus</i>			x	x		simple and complex	isolated	Yes
<i>Hylonycteris underwoodi</i>	x					simple	isolated	No
<i>Lonchorhina aurita</i>	x	x			x	simple and ?complex	isolated and clustered	No
<i>Micronycteris microtis</i>	x				x	simple	isolated and clustered	No
<i>Saccopteryx bilineata</i>	x	x			x	simple and complex	isolated and clustered	No

CHAPTER 4. SUMMARY AND CONCLUSIONS

Bats in these studies performed a wide variety of terrestrial behaviors, including such typical tetrapod gaits as the diagonal sequence walk and the bound, as well as the searching behavior and the newly described breaststrokeliike crawl. The latter two behaviors are currently described only from the Chiroptera. The behaviors of bats reported throughout this thesis are consistent with the Type 1, 2, and 3 classifications proposed by Vaughan (1970) and Schutt and Simmons (2006), with poorer walking species belonging to the Type 1 and Type 2 groups, and the terrestrially adept *Desmodus rotundus* belonging to the Type 3 group. The criteria to categorize a bat as belonging to one of the three pelvic and hindlimb morphotypes is not well defined, however, and more work must be conducted in order to establish parameters for these groupings.

Although this thesis significantly expands our knowledge of the terrestrial ability of bats, only a small sample of the more than 1,200 species of bat have ever been studied with regard to terrestrial locomotion. Fewer still have been analyzed to determine their track and trackway morphology. A continuing survey of terrestrial behavior in bats is needed to better document the variety of terrestrial abilities of bats belonging to different families, ecological niches, and morphologies. For example, *Saccopteryx bilineata* (Emballonuridae), a Type 2 bat, performed behaviors similar to those of the Type 1 bats in this study, but Lawrence (1969), Dietz (1973), and others have observed Type 2 vespertilionids, such as *Eptesicus serotinus* and *Antrozous pallidus*, to perform coordinated gaits more similar to those performed by Type 3 bats. Furthermore, *Carollia perspicillata* was observed to occasionally perform a diagonal sequence

walk, similar to that observed in some nonflying tetrapods, and future research may reveal this behavior in other Type 1 bats. Further studies must be conducted to determine the ecological and evolutionary pressures that contribute to the diversity of bat terrestrial behaviors.

Additionally, bats—the only extant quadrupedal vertebrates capable of powered flight—may be the most appropriate analog to infer pterosaur locomotion. Pterosaur and bat pelves are more similar to each other than pterosaur pelves are to those of the more closely related birds and dinosaurs (Fig. 1). In both primitive rhamphorhynchoid pterosaurs and the more advanced pterodactyloid pterosaurs, the acetabulum is oriented laterally, dorsally, and slightly posteriorly (Molnar, 1987; Wellnhofer, 1988). Pterosaurs are also reported to have produced trackways consisting of deep manus impressions and faint or nonexistent pedal impressions due to their hypothesized manus-dominated terrestrial locomotion (Unwin, 1996). This type of locomotion is similar to that observed in the bats included in these studies. The manus of pterosaurs differs from those of bats in supporting the patagium with only the fourth digit, leaving digits I–III unbound (digit V was lost through evolution), whereas bats support the patagium with digits II–V, leaving only digit I unbound (Pennycuick, 2008). This results in only a single digit impression in bat manus tracks, but three digit impressions in pterosaur manus tracks.

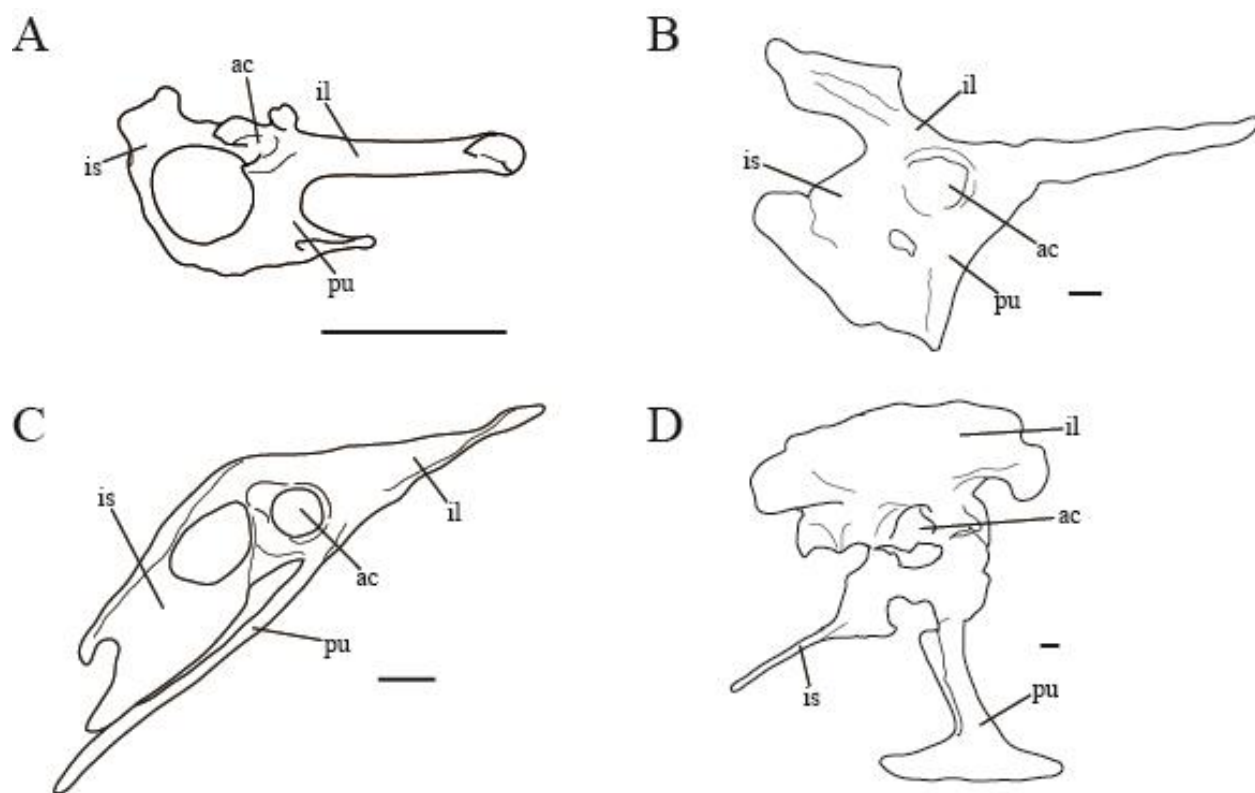


Figure 1. Comparison of bat pelvis to pterosaur, bird, and dinosaur pelvises. A) Pelvis of false vampire bat, *Vampyrus spectrum*. B) Pelvis of pterodactyloid pterosaur, *Dawndraco kanzai* (KUVF 27821). C) Pelvis of turkey vulture, *Cathartes aura*. D) Pelvis of theropod dinosaur, *Tyrannosaurus rex* (FMNH PR2081). Anatomical abbreviations: ac = acetabulum, il = ilium, is = ischium, pu = pubis. Scale bars for A, B, and C are 1 cm, scale bar for D is 10 cm.

Numerous pterosaur trackways in Lower Jurassic to Upper Cretaceous rocks are recognized throughout the world, and all preserve evidence of a quadrupedal terrestrial gait (e.g., Stokes, 1957; Wright et al., 1997; Calvo and Lockley, 2001; Hwang et al., 2002). Most of these ichnofossils preserve manus impressions with three digits oriented laterally away from the midline of the trackway, with the third digit the most elongate and oriented most caudally. This morphology results in manus impressions with the long axis parallel to the midline of the

trackway and short axis perpendicular to the midline. In this way, pterosaur manus tracks are similar to many of the manus tracks observed in casts of bat trackways, with the exception of the preservation of multiple digits in pterosaur tracks. The orientation of pedal tracks in known pterosaur trackways indicate that the digits pointed cranially (i.e., forward) during terrestrial locomotion (Chatterjee and Templin, 2004), in contrast to those of such bats as *Carollia*, which are oriented caudally (i.e., backward) (See Unwin, 1996, for figures illustrating pterosaur track and trackway morphology). The preservation or occurrence of the searching behavior in pterosaurs is, therefore, unlikely because of pedes orientation. Four to nine parallel elongate furrows associated with pes impressions of pterosaurs have been interpreted as raking traces produced by the pterosaur pes as feeding behavior (Hasiotis, 2004, 2008). These traces greatly differ from the linear and radial patterns produced by *C. perspicillata* and other Type 1 bats using the searching behavior. A Type 3 bat, such as *Desmodus*, is likely the most appropriate analog for studying pterosaur locomotion, due to the more lateral orientation of the feet, the position of the manus tracks as more distal to the trackways midline than the pes tracks, and the overall greater terrestrial competency.

Pterodactyloid pterosaur (Middle Jurassic to Late Cretaceous) locomotion may also differ from bat locomotion due to the orientation of the vertebral column. Pterodactyloid pterosaurs are hypothesized to have walked with a more upright posture, akin to the quadrupedal stance of apes (Chatterjee and Templin, 2004). The vertebral column of bats is held more parallel to the ground surface during locomotion (Altenbach, 1979). The quadrupedal posture of the more primitive rhamphorhynchoid pterosaurs (a paraphyletic group; Kellner, 2003; Unwin, 2003), however, has not been adequately studied. A detailed functional analysis contrasting bats and pterosaurs should be conducted.

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